TIMINGOFBREEDINGANDREPRODUCTIVESUCCESSINASUBARCTIC

POPULATIONOFYELLOWWARBLERS(*Dendroica petechia*)

By

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TIMING OF BREEDING AND REPRODUCTIVE SUCCESS IN A SUBARCTIC

POPULATION OF YELLOW WARBLERS (*Dendroica petechia*)

A

THESIS

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ABSTRACT.–Detailed knowledge of reproductive rates is necessary for understanding population dynamics, but this information is lacking for many populations of migratory songbirds. I examined breeding chronology and reproductive success of Yellow Warblers (*Dendroica petechia*) breeding in east central Alaska in 1997-2000. Yellow Warblers nested in both spruce forest and willow shrub habitats, but breeding density and nest success were greater in shrub habitat. Annual productivity was influenced by the number of breeding attempts per female, clutch size, success of individual eggs or nestlings, and nest success. Mean clutch size was larger than in lower latitude populations and decreased seasonally. The abbreviated breeding season limited opportunities for replacing lost clutches or broods, but enough females replaced failed nests to increase annual productivity by 0.5 fledglings per female, on average. Nest predation was likely the primary cause of nest failures and was greater on the edge between willow shrub and spruce forest than within the interior of those habitats. Timing of breeding was consistent in three years of the study, but early laying in 1998, which coincided with warmer air temperatures, effectively extended the breeding season. Extremely low nest success lowered annual productivity in 1998, despite the extended breeding season.

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INTRODUCTION

Passerine birds are a biologically significant resource in many ecosystems, functioning as important predators of insects and other arthropods (Marquis and Whelan 1994, Greenberg et al. 2000), disseminating plant seeds and pollen (Jordano 1982, Borgells et al. 2001, Paulsen and Högstedt 2002), and serving as prey for a variety of predators (Joy et al. 1994, Farnsworth and Simons 2000, Helldin 2000). Recently, there has been concern that many species of passerines, particularly those that migrate between the Neotropical and Neararctic regions, are experiencing population declines (Robbins et al. 1989, Askins et al. 1990). Uncertainty about the causes of these declines has highlighted the general lack of detailed knowledge of breeding biology, demography, and ecological requirements of many passerines species (Askins et al. 1990, Martin 1992, Sherry and Holmes 1995). Conservation and management of migrant songbirds will depend upon understanding what features of their biology and environment promote growth and persistence of populations.

Although there has been increased emphasis on studying demography of passerine populations in recent years (e.g., Holmes et al. 1996, Budnik et al. 2000, Murphy 2001), little is known about productivity of populations breeding in Alaska. Breeding at high latitudes can provide some unique challenges for avian populations, including longer distances to travel during migration (Bell 1997), a restricted breeding season (Morton 1976, Benson and Winker 2001), and increased risk of experiencing harsh weather conditions while breeding (Eeva et al. 2000). The abbreviated breeding

season constrains productivity, but abundant seasonal food resources, an extended summer photoperiod, minimal habitat disturbances, and a less diverse suite of potential nest predators may allow enhanced productivity within the constrains of this limited breeding season.

Many studies have examined the breeding biology of passerines nesting at northern latitudes in Europe (e.g., Slagsvold 1976, Orell and Ojanen 1983, Eeva et al. 2000), but little information is available on how the conditions at higher latitudes influence nesting ecology of species breeding in the northern regions of North America. This information could provide a baseline for monitoring the effects of changes in habitat or climate on these populations. Already, changes are being observed in the timing of breeding for some lower latitude populations in response to a warming trend in spring air temperatures that may be a result of long-term climatic change (Brown et al. 1999, Dunn and Winkler 1999). Habitat modification or fragmentation is changing the quality of habitats and increasing the risk of nest predation, thus having a negative impact on the reproductive success of many passerine species nesting in temperate areas (Hoover et al. 1995, Burke and Nol 2000, Vierling 2000). Habitat fragmentation is also exacerbating the impact of the Brown-headed Cowbird (*Molothrus ater*), a brood parasite, on the reproductive success of many mid-latitude populations (Brittingham and Temple 1983). The relatively pristine condition of many habitats in Alaska could provide opportunities to compare demographic characteristics of populations breeding in habitats that have not been modified by humans to those breeding in disturbed habitats to assess the impact of these disturbances.

The Yellow Warbler (*Dendroica petechia*) is a small, insectivorous passerine that breeds throughout most of North and Central America and into northern South America (DeGraaf and Rappole 1995). The subspecies that breed in North America are highly migratory, nesting as far north as the Brooks Range in Alaska (Kessel and Gibson 1978) and the Mackenzie River Delta in northern Canada (Godfrey 1986) and wintering from Mexico to central Peru and northern Brazil (American Ornithologists' Union 1983). The Yellow Warbler has been the subject of several studies, but surprisingly little detailed demographic information is available for this widespread species (see review in Lowther et al. 1999). Population status of the Yellow Warbler varies throughout its range. Populations in eastern United States appear to be relatively stable (Dunn and Garrett 1997), but populations in the western United States are declining as natural riparian habitats are being modified or destroyed (Ohmart 1994).

During the summers of 1997-2000, I examined the nesting ecology of Yellow Warblers breeding at a study site in east central Alaska. The objectives of my study were to increase knowledge of the breeding biology of a migratory passerine nesting in Alaska, describe the breeding schedule of this species at a relatively high latitude, examine the various components of reproductive success, assess their contribution to annual productivity for the study population, and investigate the relationship between latitude, timing of breeding, and reproductive success. Reproductive measures that I studied included the onset of egg laying, clutch size, duration of nesting, success of individual eggs and nestlings, success of nests, frequency of breeding attempts per female, annual productivity per female, habitat use, and breeding density.

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CHAPTER I. TIMING AND DURATION OF BREEDING IN A SUBARCTIC
POPULATION OF YELLOW WARBLERS[1]

ABSTRACT.–I documented the breeding chronology of Yellow Warblers
(*Dendroica petechia*) nesting at Canvasback Lake, Alaska (66° 23'N, 146° 23'W) in
1997-2000. The brief summer at high latitudes constrains the time available for
breeding, particularly for long distance migrants. Yellow Warblers began arriving at
the study site in late May. Clutches were initiated between 27 May and 30 June, with
50% of all clutches started between 6 and 15 June. All young had fledged by 25 July;
pre-basic molt began in early July, and adults departed the study area in late July and
early August. A breeding pair averaged 28 days for nest construction and completion
of a successful nesting effort. Pairs attempted to raise only one brood per season, but
sometimes replaced clutches, and more rarely broods, that failed. The period during
which replacement clutches were initiated was limited. The onset of laying was earlier
in 1998 than in the other years; early breeding coincided with warmer air temperatures
during April and May and earlier migration dates through Fairbanks, Alaska. The
breeding season of the Yellow Warbler at the study site was compressed; the period
between arrival and the onset of breeding was brief, and the onset of remigial molt
overlapped with the fledgling care period.

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INTRODUCTION

Birds that breed at high latitudes must contend with highly seasonal environments. The period when ambient temperatures remain above freezing and conditions are favorable for breeding is brief. Species that are resident throughout the year or migrate relatively short distances are able to adjust the timing of their breeding activities to coincide with the start of favorable environmental conditions during a given spring (James and Shugart 1974). Spring arrival dates of long distance migrants tend to be later, usually coinciding with the average date when conditions are first favorable for breeding (Johnson and Herter 1990, Hagan et al. 1991). The later spring arrival dates and earlier fall departure dates of long distance migrants limit the duration of their breeding seasons, particularly at high latitudes.

For long distance migrants to successfully produce young and complete pre-basic molt during an abbreviated breeding season, different stages of the annual cycle may overlap or be compressed or delayed. Individuals may reduce the period between arrival and the onset of breeding (Williamson and Emison 1971, Morton 1976) and initiate breeding earlier relative to vegetation phenology (Slagsvold 1976, Eeva et al. 2000). Females may reduce clutch size, thus reducing the duration of the nesting interval (Järvinen and Lindén 1980). Molt may overlap with nesting activities (Tiainen 1981, Orell and Ojanen 1980, Hemborg 1999) or migration (Dolnik and Blyumental 1967, Eeva et al. 2000). The time needed to conduct molt may be compressed (Morton

et al. 1969, Williamson and Emison 1971, Eeva et al. 2000). Alternatively, individuals may suspend or delay molt until they reach their wintering areas (Holmes 1966).

The Yellow Warbler (*Dendroica petechia*) is a small, insectivorous passerine that breeds throughout most of North America, mostly in wet shrub thickets, deciduous woodlands, shrubby forest edges, and second-growth habitats (Bent 1953, Schroeder 1982, Peck and James 1987). Pairs breed as far north as the Brooks Range in Alaska (69° N, West and White 1966) and the Mackenzie River Delta of northern Canada (68° N, Salter et al. 1980), and Yellow Warblers winter in the tropics from Mexico to central Peru and northern Brazil (Dunn and Garrett 1997). Most information available on the breeding biology of the Yellow Warbler has been obtained from populations breeding in temperate areas (e.g., Goossen and Sealy 1982, Mitra 1999). Information is limited for populations breeding in northern areas, mostly in the form of species accounts (e.g., Kessel 1989), but two studies have occurred in the subarctic environment of the Hudson Bay area (Rimmer 1988, Briskie 1995). In east central Alaska, the Yellow Warbler is a relatively late spring and early fall migrant and has one of the most restricted breeding seasons of many of the passerine species that breed in this region, including other long-distance migrants (Keast 1980, Benson and Winker 2001).

During this study I examined the timing of breeding for Yellow Warblers (*D. p. banksi*, Browning 1994) nesting in east central Alaska. The eastern part of central Alaska has a subarctic, continental climate that is characterized by extreme seasonal variation in temperature and day length and a restricted growing season (U. S. Department of Interior, 1974). My main objectives were to determine the timing and

duration of breeding for a subarctic population of Yellow Warblers, investigate

interannual variation in breeding chronology, and compare breeding chronology of the

study population to that of populations in other areas.

METHODS

Study Area.–I studied the nesting biology of Yellow Warblers at Canvasback

Lake (66° 23'N, 146° 23'W) on the Yukon Flats National Wildlife Refuge, Alaska

during the summers of 1997-2000. Canvasback Lake is a large, highly productive

wetland surrounded by a mixture of coniferous and broadleaf forests, willow shrub

thickets, grass and sedge meadows, and wet herbaceous marshes. The lake is located in

a region that has a frost-free period of approximately 126 days; the average minimum

daily temperature at Fort Yukon, which is approximately 55 km northeast of the study

site, exceeds 0°C from 14 May to 16 September (Western Regional Climate Center,

1961-1990). The study site also has essentially 24 hours of light from 10 May through

2 August, because long periods of twilight effectively extend the day length (U. S.

Naval Observatory 2001). The breeding season is relatively brief, but warm

temperatures and long days during the summer trigger an intense flush of vegetative

growth and insect production (U. S. Department of Interior, 1974).

Nest Searching and Monitoring.–A field assistant and I intensively searched for

nests on a 12-ha study plot in the mixed shrub and forest habitat on the west shore of

Canvasback Lake in 1997-2000. We marked the study plot at 25-m intervals to provide

a grid for systematic nest searching and a reference for mapping nests. Nest searches were conducted once or twice each week from late May to mid-July. Additional areas of similar habitat were searched on the south shore of the lake in 1998 and 1999. Following Martin and Geupel (1993), nests were found by observing adult behavior and by visual searches of potential nest substrates.

We monitored the status of each nest every 3-5 days to provide information on nesting chronology. The timing of egg laying, hatching, and fledging was determined either by direct observation or by backdating using mean incubation or nestling intervals and known egg laying, hatching, or fledging dates. Clutch initiation was the day the first egg was laid in a nest. Clutch size was determined after laying was complete and before hatching began.

A nest was considered successful if at least one young fledged from the nest. If a nest failed, I continued to observe the behavior of adults in the area to determine if a replacement clutch was initiated. Some replacement nests were easily identified by the presence of color-banded adults, but, on average, only 30% of the females and 50% of the males observed at nests were color banded. I classified additional nests as replacements by the following criteria: (1) the distance between nests was ≤ 20 m or both nests were on the same breeding territory and (2) the interval between failure of one nesting attempt and initiation of the other clutch was ≤ 7 days. The preceding criteria were consistent with observations of multiple nesting attempts of color-banded individuals. Additionally, a female observed using the material from one nest to build another was assumed to have built both nests.

Banding and Color Marking.–The staff of Yukon Flats National Wildlife Refuge captured Yellow Warblers at my study site between 10 June and 1 August as part of an on-going mark-recapture study using the protocol of the Monitoring Avian Productivity and Survivorship (M.A.P.S.) program (Burton and DeSante 1998). During May and June of 1998 and 1999, a field assistant and I conducted additional localized mist netting in an effort to increase the proportion of marked individuals. Warblers were banded with a standard federal aluminum leg band and were aged and sexed using the techniques described by Pyle (1997). If time allowed, we also recorded the presence or absence of remigial molt in captured individuals. The timing of remigial molt was considered to be representative of the timing of pre-basic molt, because Yellow Warblers replace virtually all body feathers during the period of remigial molt (Rimmer 1988). I color marked adult Yellow Warblers that had a noticeable brood patch or cloacal protuberance with a unique combination of colored leg bands that was randomly assigned to each individual. Observations of color-marked adults matched individuals with specific nests, mates, or fledglings.

Temperature.–To investigate the effect of weather on the onset of breeding, I examined the relationship between ambient temperature and the initiation dates of first clutches at Canvasback Lake. I obtained daily air temperatures at Fort Yukon, Alaska (66° 34'N, 145° 16'W) from the National Weather Service in Fairbanks, Alaska for the months of April, May, and June. Since data for average daily temperatures were frequently missing, I calculated average daily temperatures by averaging the minimum and maximum daily temperatures.

Data Analysis.–Statistical analyses were performed using the SAS statistical package, version 8.2 (SAS Institute 2001). I used Julian dates for all analyses involving dates, and comparisons among years were restricted to nests found on the study plot. Nonparametric analyses were used if the data violated the assumptions of normality or homoscedasticity. I used analysis of variance (ANOVA; PROC GLM, type III sums of squares) and the Tukey test to examine variability among and between years in average monthly temperatures for April, May, and June. I compared the distribution of initiation dates of first clutches among years using multiple Kolomogorov-Smirnov (K-S) two-sample tests (PROC NPAR1WAY, EDF option). The Bonferroni method was used to adjust the rate of experiment-wide error for these multiple pair-wise comparisons. I examined variation in the duration of a successful nesting attempt among years using analysis of covariance (ANCOVA; PROC GLM, type III sums of squares), including clutch initiation date as a covariate. I used linear regression (PROC REG) to illustrate the relationship between nesting interval and initiation date. I used logistic regression (PROC LOGISTIC) to assess the relationship between the date a nesting attempt failed and the probability that the nest would be replaced. All tests were two-tailed and were considered statistically significant for $P < 0.05$. Means are presented as $\pm$ standard error (SE). Sample sizes differ among analyses because complete information was not available for every nest.

RESULTS

Temperature.–The mean of average daily temperatures for April was significantly warmer in 1998 than in each of the other three years (one-way ANOVA, $F = 6.38$, $P < 0.01$; Tukey tests of 1998 vs. 1997, 1999, or 2000, $P < 0.05$ for each pair). The mean of average daily temperatures for May also differed among years ($F = 6.76$, $P < 0.01$) but was significantly different only between 1998 and 2000 (Tukey test, $P < 0.05$). In 1998, the mean monthly temperatures for April and May were 7 and 3°C above normal, respectively, while the mean monthly temperature for May 2000 was almost 2°C below normal (Fort Yukon climate normals, 1938-1990; Western Regional Climate Center 2001). During June, the mean of average daily temperatures did not differ significantly among the four years ($F = 1.95$, $P = 0.13$). A comparison of the distributions of average daily temperatures among months and years is presented in Figure 1.1.

I calculated a spring warmth index for each year by calculating the cumulative sum of average daily air temperatures that were above a threshold of 0°C (Fig. 1.2). Ambient temperatures first warmed above 0°C on 7 April, 4 April, 16 April, and 20 April in 1997, 1998, 1999, and 2000, respectively (National Weather Service, Fairbanks, Alaska). Temperature sums were terminated on 10 June, the four-year median date for the initiation of first clutches. The period between 1 April and 10 June included ice break-up on rivers and lakes, foliage green-up, and the onset of insect emergence. The cumulative temperature sums for the spring of 1998 exceeded those of

the other three years, indicating that air temperatures warmed up earlier in that year. Cumulative temperature sums were relatively similar in 1997 and 1999. In 2000, the cumulative temperature sum was lower during late May than in the other three years, indicating that air temperatures were cool during the arrival period of Yellow Warblers at Canvasback Lake.

Arrival.–I was unable to document arrival dates for Yellow Warblers at my study site, but I assumed they were similar to the dates Yellow Warblers passed through Fairbanks, Alaska (64°50' N, 147°50' W), approximately 185 kilometers south of Canvasback Lake. During spring migration at Creamer's Field Migration Station (CFMS) in Fairbanks, migrating Yellow Warblers have been captured as early as 15 May and as late as 14 June, but the majority of the migrants (59%) pass through CFMS between 24 May and 3 June (median = 31 May, n = 166 individuals, 1992-2000; Alaska Bird Observatory [ABO] unpubl. data). During the four years of this study, the annual median date of spring passage for Yellow Warblers at CFMS ranged from 25 May in 1998 to 8 June in 2000 (Table 1.1).

Timing of Breeding.–Egg laying began on 5 June, 27 May, 31 May, and 5 June in 1997, 1998, 1999, and 2000, respectively. A mean interval of 7 ± 2 days separated the median date of spring migration passage at CFMS and the median date of egg laying for first clutches at Canvasback Lake during the four years of my study (Table 1.1). Fifty percent of all clutches observed in 1997-2000 were started between 6 and 15 June (median = 10 June, mean = 10 June ± 0.5 days, n = 227; Fig. 1.3). Fewer than 10% of all clutches were initiated after 20 June and no clutches were initiated after 30

June. Hatching occurred between 9 June and 11 July (mean = 23 June ± 0.5 days, n =

159) and fledging occurred between 18 June and 26 July (mean = 2 July ± 0.6 days, n =

110). More than 90% of broods had fledged by 10 July. Young remained dependent

upon the adults for an unknown period of time after fledging, but adults were still

feeding fledglings 14-19 days after the last young had fledged from their nests (n = 13

broods).

I examined annual variation in the onset of breeding by comparing initiation

dates for first clutches among years. The distribution of initiation dates was skewed

left, and initiation dates were significantly earlier in 1998 than in the other three years

(two-sample K-S tests: $P < 0.01$ for each pair of comparisons; Table 1.2 and Fig. 1.3).

The median initiation date was 10 days earlier in 1998 (31 May) than the three-year

median for 1997, 1999, and 2000 (10 June). Two color-marked females that were

observed in both 1997 and 1998 initiated their first clutches 11 and 13 days earlier in

1998 than in 1997.

Nesting Interval.–Female Yellow Warblers began nest construction 5.1 ± 0.4

days before laying their first egg (range = 4-7 days, n = 9 nests). Eggs were usually laid

on successive days until clutch completion, a period of 3-6 days. One exception to this

pattern was observed; a female laid a replacement clutch of 5 eggs during a period of 7

days. Females were occasionally observed on nests during the laying period (41 of 218

visits to nests during laying), so I was unable to document the start of steady incubation.

The first eggs of a clutch usually hatched 7-9 days after the clutch completion date

(exact dates of clutch completion and first hatch known for 12 nests, mean interval =

8.8 ± 0.2 days). Hatching appeared to be asynchronous; at least 10 clutches were known to have taken more than 24 hours to complete hatching. Young remained in the nest 8-12 days, with first fledging averaging 9.1 ± 0.2 days after the first young had hatched (exact dates of first hatch and first fledge were known for 19 broods). The amount of time needed for all young in a particular brood to fledge appeared to be highly variable. The young of 14 broods required more than 48 hours to complete fledging, with the maximum interval between fledging of first and last young being about four days. Thirteen broods completed fledging after more than 20 hours. Of the remaining 7 broods that were observed during the fledgling interval, 5 broods fledged within 30 hours and 2 fledged within 20 hours.

The duration of successful nesting attempts from laying of the first egg to fledging of the last young (hereafter "nesting interval") ranged from 19 to 27 days, with a mean of 23.2 ± 0.1 days (n = 105). For nests found on the study plot, the nesting interval declined as the season progressed, decreasing by 0.8 days for every ten-day delay in the onset of egg laying ($r^2 = 0.17$, $F = 18.84$, n = 95, $P < 0.01$; Fig. 1.4). I excluded one outlier from the analyses, a late clutch initiated on 30 June 2000, because the incubation period of this clutch was unusually prolonged (> 10 days). The nesting interval did not differ significantly among years nor was there a significant interaction between year and initiation date (Table 1.3).

Replacement Nests.–At least 46% of the nests (99 of 215) found on the study plot failed during the four years of this study, but females replaced 40% (40 of 99) of the clutches or broods that were lost. The probability that a failed breeding attempt

would be replaced declined as the season advanced (logistic regression coefficient = -0.17, n = 128, Wald χ^2 = 26.51, df = 1, P < 0.01). Breeding attempts that were replaced failed 12 days earlier, on average, than those that were not replaced. Clutches were more likely to be replaced than broods. Seventy-three percent (11 of 15) of the clutches that failed during laying and 49% (19 of 39) of the clutches that failed during incubation were replaced, but only 28% (8 of 29) of the broods that were lost were replaced. Half of all clutch replacements occurred in 1998, and more broods were replaced in 1998 (6 of 14) than in the other three years combined (2 of 15). Three females, each in a different year, replaced two failed clutches with a third. Only 4 clutches and 2 broods that failed after 15 June were replaced.

Construction of a new nest usually started within a day of failure of the previous nest. With one exception (1 of 45), females did not re-use a nest cup from which a clutch or brood had been lost, but four females were observed removing materials from a failed nest to build a new one. The first egg of a replacement clutch was laid 4-7 days (mean = 5.7 ± 0.3, n = 16) after the failure of the first clutch or brood. The earliest date for the initiation of a replacement clutch was 1 June 1998, and the median date of initiation for all replacement clutches was 17 June (n = 43).

Post-breeding Schedule.–Remigial molt was observed as early as 1 July in adult Yellow Warblers (3 males and 3 females) that were captured in mist nets at the Canvasback Lake MAPS station; all 3 females had receding brood patches and were probably failed breeders. Nearly 50% (38 of 77 individuals) of the captured adults for which the molt status was recorded had started remigial molt by 13 July. Remigial molt

overlapped with the fledgling care period for at least some of the warblers that nested on the study plot (8 of 22 individuals). One female had new first primary feathers erupting (< 2 mm in length) the day before her young fledged from the nest. Although the duration of the remigial molt period was not recorded, one male that was captured 35 days after the last nestling had fledged from his nest was growing his ninth primaries and first secondaries and all of his rectrices. Adults began disappearing from the study site in mid-July, and few Yellow Warblers were observed after the first week of August.

DISCUSSION

A typical female breeding at Canvasback Lake required an average of 28 days to construct a nest and complete a successful nesting attempt. I did not measure the extent of the molting period at my study site, but it may have been similar to the period of 37 days required, on average, by female Yellow Warblers breeding at James Bay, Ontario (Rimmer 1988). If pre-basic molt was initiated immediately after young had fledged from the nest, the average female breeding at Canvasback Lake would require approximately 65 days to complete both successful nesting and remigial molt. Benson and Winker (2001) estimated that the duration of the breeding season for Yellow Warblers nesting in east central Alaska is approximately 84 days. Because a difference of only 19 days exists between the duration of the breeding season and the amount of time needed to complete nesting and molt, there is not much flexibility in the timing of breeding season activities at this latitude.

Specific information on the duration of different stages of the nesting cycle for Yellow Warblers breeding in other areas is limited and sample sizes tend to be small, but the nesting interval at Canvasback Lake was comparable to other areas. Nest construction spanned 6.2 ± 1.1 days in northern Manitoba (n = 5; Briskie 1995) and 6.3 ± 0.5 days in Rhode Island (n = 37, Mitra 1999), slightly longer than the mean period of 5 days at my study site. In southern Manitoba, young fledged from the nest 8.2 ± 0.2 days (n = 12) after the first egg hatched (Goossen 1978), while young fledged after 8.5 ± 0.2 days (n = 14) in northern Manitoba (Briskie 1995); these values were slightly less than the mean of 9.1 days observed at Canvasback Lake.

It was more problematic to make direct comparisons of incubation periods between sites. During this study, I defined the incubation period as beginning on the day the last egg was laid and ending when the first egg hatched (Martin et al 1997, Nur et al. 1999), because the behavior of the adults at the nest probably changed after at least one egg had hatched. Other studies have defined the incubation period as the laying of last egg until hatching of last young (Nice 1953). Since I did not record the duration of the hatching interval at my study site, I could not make comparisons to studies that used the other definition of the incubation period unless they also reported a known hatching interval. In southern Manitoba, the mean interval from laying of the last egg until hatching of the last young was 11.3 ± 0.1 days (n = 15; Goossen 1978), while the mean hatching interval was 1.5 ± 0.1 days for 4-egg clutches (n = 19) and 2.1 ± 0.1 days for 5-egg clutches (n = 21; Hébert 1993). Therefore, the mean interval from laying of the last egg until hatching of the first young was approximately 9.2-9.8 days

for Yellow Warblers in southern Manitoba, which was comparable to the mean interval of 8.8 days that was observed at Canvasback Lake. In northern Manitoba, however, the mean interval from laying of the last egg until hatching of the last young was 11.7 ± 0.2 days (n = 15), and most clutches (77%) hatched within 24 hours (n = 26; Briskie 1995). The interval from laying of the last egg until hatching of the first young was approximately 10.7 days, almost two days longer than the mean interval at Canvasback Lake.

The nesting interval is relatively invariant in many species of passerines that use open-cup nests, because these species have already evolved rapid rates of development to minimize the amount of time young are in the nest and vulnerable to predators (Bosque and Bosque 1995, Martin 1995). The nesting intervals for Yellow Warblers at other locations were within range of the values that were observed at my study site. The nesting interval at my site did decrease as the season progressed, probably as a result of the seasonal decline in clutch size. Many species of birds experience a seasonal decline in clutch size (Klomp 1970, Hussell 1972, Hochachka 1990), and decreasing clutch size would be one adaptation individuals could have to decrease the duration of nesting.

The nesting interval of Yellow Warblers did not appear to be very compressible, but other portions of the annual breeding cycle can be compressed more readily. Females in many populations that breed at higher latitudes or altitudes have reduced the number of days between arrival at their breeding territories and the onset of laying (Morton 1976, Keast 1990). The brief interval between spring migration dates at

Fairbanks and the initiation of laying at Canvasback Lake suggests that, on average, female Yellow Warblers began nest construction less than 7 days after arriving on their breeding territories (see Table 1.1). By the end of May, the Yukon Flats is receiving 24 hours of daylight, the average daily air temperature exceeds 0°C, leaves are unfurling on deciduous trees and shrubs, and most, if not all, of the ice has disappeared from lakes (U. S. Department of Interior, 1974, Bayha and Wolfe 1999). Average conditions favor the immediate onset of breeding given the observed arrival dates.

Another stage of the annual cycle that can be compressed is the post-breeding schedule. Many adult migratory passerines undergo a complete pre-basic molt, involving all body and flight feathers, while on their breeding grounds (Pyle 1997). Growing new feathers is an energetically costly process, so most migratory birds separate molt from breeding activities (Payne 1972). Individuals of some species that breed at high latitudes, however, are able to overlap their breeding and molt schedules (Holmes 1971, Hussell 1972, Orell and Ojanen 1980, Tiainen 1981, Orell and Ojanen 1983), probably because the abundant food resources available during the summer at these high latitude locations enable individuals to meet the increased energetic demands of overlapping breeding and molt. At Canvasback Lake, at least one female began primary molt before her young had fledged; she initiated her clutch at a relatively late date (18 June). Other Yellow Warblers began their pre-basic molt while they were caring for fledglings. Rimmer (1988) also reported overlap between molt and fledgling care for Yellow Warblers nesting at James Bay, Ontario, another high latitude population. Additionally, Benson (2000) reported that 63% of the Yellow Warblers

captured during fall migration at Fairbanks, Alaska were still in pre-basic molt.

Considering the total disappearance of adult Yellow Warblers from my study site by 10

August (pers. obs.), it seems likely that Yellow Warblers leave Canvasback Lake before

they have completed their pre-basic molt. Consequently, the overlap between molt and

other portions of the annual cycle allowed further compression of the breeding schedule

at Canvasback Lake.

A high proportion of passerine clutches or broods is lost to nest predators or

weather-related events (Nice 1957, Murphy 1983, Ricklefs 1969, Martin 1992).

Females of many species, including Yellow Warblers, will readily replace clutches that

have failed (Morton et al. 1972, Nolan 1978, Weatherhead 1979, Goossen and Sealy

1982, Holmes et al. 1992, Orell and Ojanen 1983, Murphy 1996, Sherry and Holmes

1997, Mitra 1999). At Canvasback Lake, only half of the clutches or broods that were

lost on the study plot were replaced, and females rarely attempted to replace more than

one lost clutch or brood. The probability of replacement rapidly decreased as the

season progressed, implying there was a time constraint on when clutches could be

initiated.

Populations breeding at higher latitudes often have fewer opportunities to

replace failed clutches or broods (Weatherhead 1979) than those breeding at more

temperate latitudes (Nolan 1978, Holmes et al. 1992). Female Yellow Warblers nesting

in southern Manitoba were able to lay as many as three replacement clutches in one

season (Sealy, Briskie, and Biermann 1986). In a given year, however, the duration of

the egg laying period may be influenced by climatic conditions which favor greater or

lesser rates of clutch replacement (Morton et al. 1972). At Canvasback Lake, the early onset of breeding in 1998 allowed increased opportunities for nest replacement; 50% of all replacement attempts occurred in 1998, including 75% of the brood replacements.

At my study site, many clutches were initiated earlier in 1998 than in the other three years (Figure 1.3). This early onset of laying coincided with warmer air temperatures during late spring (April and May). Breeding frequently begins earlier in warmer springs than in cooler springs for a variety of species (Nolan 1978, Goossen and Sealy 1982, Orell and Ojanen 1983, Fox et al. 1986, Briskie 1995, Wesolowski 1998, Meijer et al. 1999, Eeva et al. 2000). In seasonal environments, heat accumulation in the spring must exceed a certain minimum threshold level to trigger foliage development and insect emergence (Jackson 1966, Danks and Oliver 1972). A positive relationship has been observed between the advancement of habitat phenology and/or the increase in food availability and the onset of egg laying for a number of passerine populations (Hussell 1972, Bryant 1975, Slagsvold 1976, Greenlaw 1978, Murphy 1986, Blancher and Robertson 1987, Clamens 1990, Blondel et al. 1993). At Canvasback Lake, the rate of foliage development was noticeably earlier in 1998 than in the other three years (pers. obs.), indicating that environmental conditions were probably propitious for early breeding.

Favorable spring climatic conditions in 1998 may also have facilitated migration and advanced spring arrival dates (Richardson 1978, 1990), enabling more individuals to initiate breeding at an earlier date. Early breeding can be advantageous because individuals will have more time to nest, raise young, molt, and prepare for fall

migration. Spring capture dates were somewhat earlier at CFMS in 1998 compared to the other three years (see Table 1.1). Temperatures were warmer than normal across the continent during the first half of 1998, probably a response to the strong 1997-98 El Niño/Southern Oscillation event (Duffy and Bryant 1998). Large-scale atmospheric conditions can influence the progress of migration for both short and long distance migrants (Forchhammer et al. 2002). Arrival dates of long distance migrants, however, tend to be less plastic than those of shorter distance migrants (Hagan et al. 1991), so these migrants are constrained in how much they can advance their egg laying dates by the timing of their arrival at the breeding areas (Both and Visser 2001).

In May of 2000, air temperatures near the study site were cooler, on average, than in the other three years (Fig. 1.1), and the median spring capture date for Yellow Warblers at CFMS was the latest median date recorded in nine years (ABO, unpubl. data). Despite these indications that environmental conditions may not have been as favorable in the spring of 2000 as in the other three years, the onset of laying at Canvasback Lake did not average significantly later than those years. In fact, earliest egg laying dates at Canvasback Lake preceded first arrival dates at CFMS (Table 1.1). Because the number of Yellow Warblers captured in Fairbanks during spring migration was small, dates of capture at CFMS provided a relatively coarse index of arrival dates at Canvasback Lake and may not have been as representative of arrival in 2000. If some individuals arrived later than average, however, they may have compensated by further reducing the period between arrival and the onset of laying, because delayed

breeding can be detrimental to the reproductive success of individuals that have an abbreviated breeding season (Johnson and Herter 1990, Eeva et al. 2000).

The timing of breeding of Yellow Warblers has been studied at several locations, including Delta Marsh, Manitoba (50° 11' N; Goossen and Sealy 1982), James Bay, Ontario (51° 29' N; Rimmer 1988), Churchill, Manitoba (58° 40' N; Briskie 1995), and Great Swamp of Rhode Island (41° 27' N; Mitra 1999). Of these four sites, the range of clutch initiation dates at Canvasback Lake was most similar to Delta Marsh in southern Manitoba, despite the 16° difference in latitude (Table 1.4). Although the Yukon Flats region is bisected by the Arctic Circle (66°), it has a continental climate, and the mountains surrounding the region isolate the Flats from many weather systems affecting neighboring areas (Gallant et al. 1995). Temperatures tend to warm up quickly as day length increases, and the average temperatures at Fort Yukon in June and July are similar to those near Delta Marsh (Fig. 1.5; temperature normals from Environment Canada 1998 and Western Regional Climate Center 2001). For the other sites, earliest clutch initiation occurred in Rhode Island, which is well south of the boreal forest zone, and the latest nesting occurred near Hudson Bay in Canada (Churchill and James Bay).

The Hudson Bay area has an arctic climate, despite its more temperate latitude; air temperatures in June and July are strongly influenced by the amount of ice that remains in the bay and the prevailing wind direction (Rouse 1991). The earliest egg laying dates reported for Yellow Warblers nesting at Churchill and James Bay were 15-18 days later than the earliest laying date at Canvasback Lake (Table 1.4). In a similar

comparison, Hussell (1972) reported that Lapland Longspurs (*Calcarius lapponicus*) breeding at Churchill, Manitoba (58° N) had a mean clutch initiation date 15 days later than that of longspurs nesting near Eagle Creek in central Alaska (66° N). Yellow Warblers breeding at Churchill also had a longer incubation period, on average, than those nesting at Canvasback Lake (see earlier discussion). Although individuals nesting in northern Manitoba appear to be even more time-constrained than those nesting at Canvasback Lake, they are also exposed to harsher weather conditions. Eggs may cool to a greater extent when a female is off the nest, prolonging the incubation interval. Briskie (1995) reported that Yellow Warbler nests at Churchill had thicker walls than those in southern Manitoba, indicating that individuals were compensating for the cooler climate by increasing the insulation of their nests.

In central Alaska, the Yellow Warbler has one of shortest breeding seasons of the species that commonly nest in this region, including other long distance migrants (Benson and Winker 2001). This abbreviated breeding season has imposed constraints on the timing of breeding season activities (pair formation, nesting, fledgling care, and pre-basic molt), such that breeding activities are more tightly scheduled than those of lower latitude populations. Individuals can compensate for scheduling constraints by reducing the duration of these activities. At Canvasback Lake, Yellow Warblers have a relatively brief period between arrival and the onset of laying and between nesting and the onset of molt. The duration of the nesting interval, on the other hand, was similar to that of lower latitude populations. Yellow Warblers nesting at Canvasback Lake were not so strictly constrained by the brevity of their breeding season that some individuals

could not replace lost clutches or even broods. If Yellow Warblers did not attempt to replace failed clutches, they could adapt to an even more restricted breeding season. This adaptability may explain why Yellow Warblers are able breed as far north as the Brooks Range in northern Alaska (69° N; Kessel and Gibson 1978), an area with an arctic climate and, consequently, a more abbreviated breeding season than occurs at Canvasback Lake.
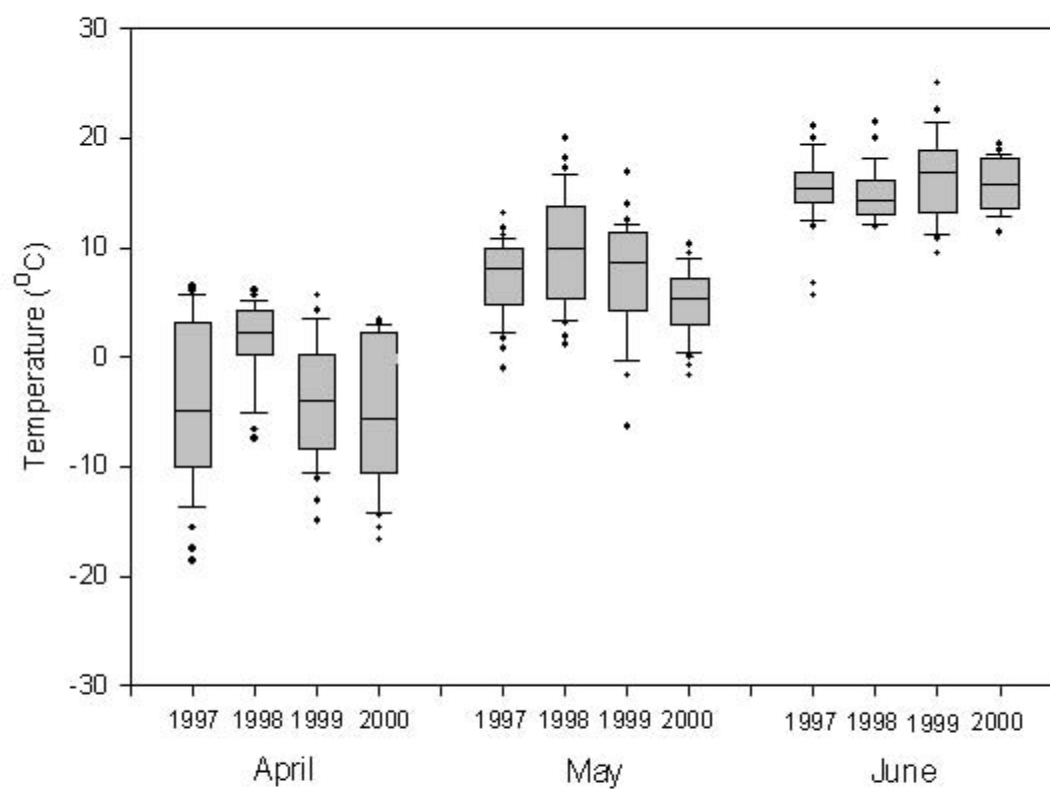
FIGURE 1.1. Average daily temperatures at Fort Yukon, Alaska for the months of April, May, and June in 1997-2000. Medians (central lines in boxes), 25-75% ranges (boxes), 10th and 90th percentiles (whiskers), and outliers (dots) are shown.
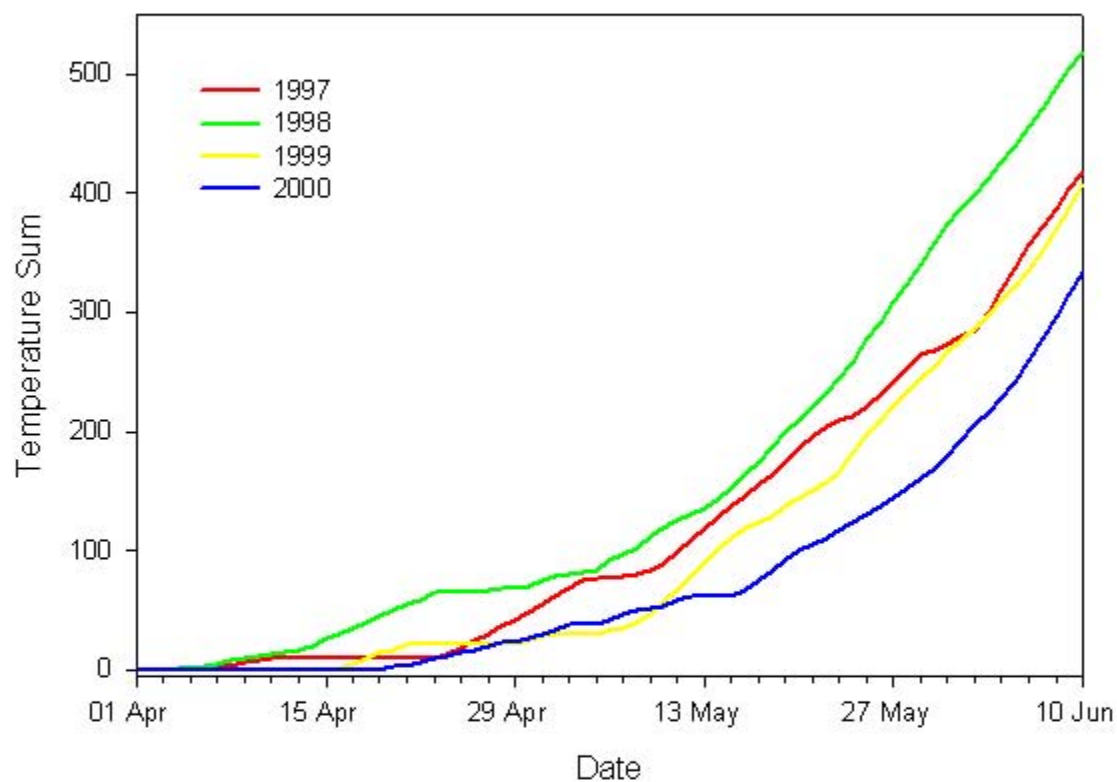
FIGURE 1.2 Cumulative sum of degrees (^{o}C) above freezing for average daily temperatures at Fort Yukon, Alaska for the period of 1 April to 10 June, 1997-2000.
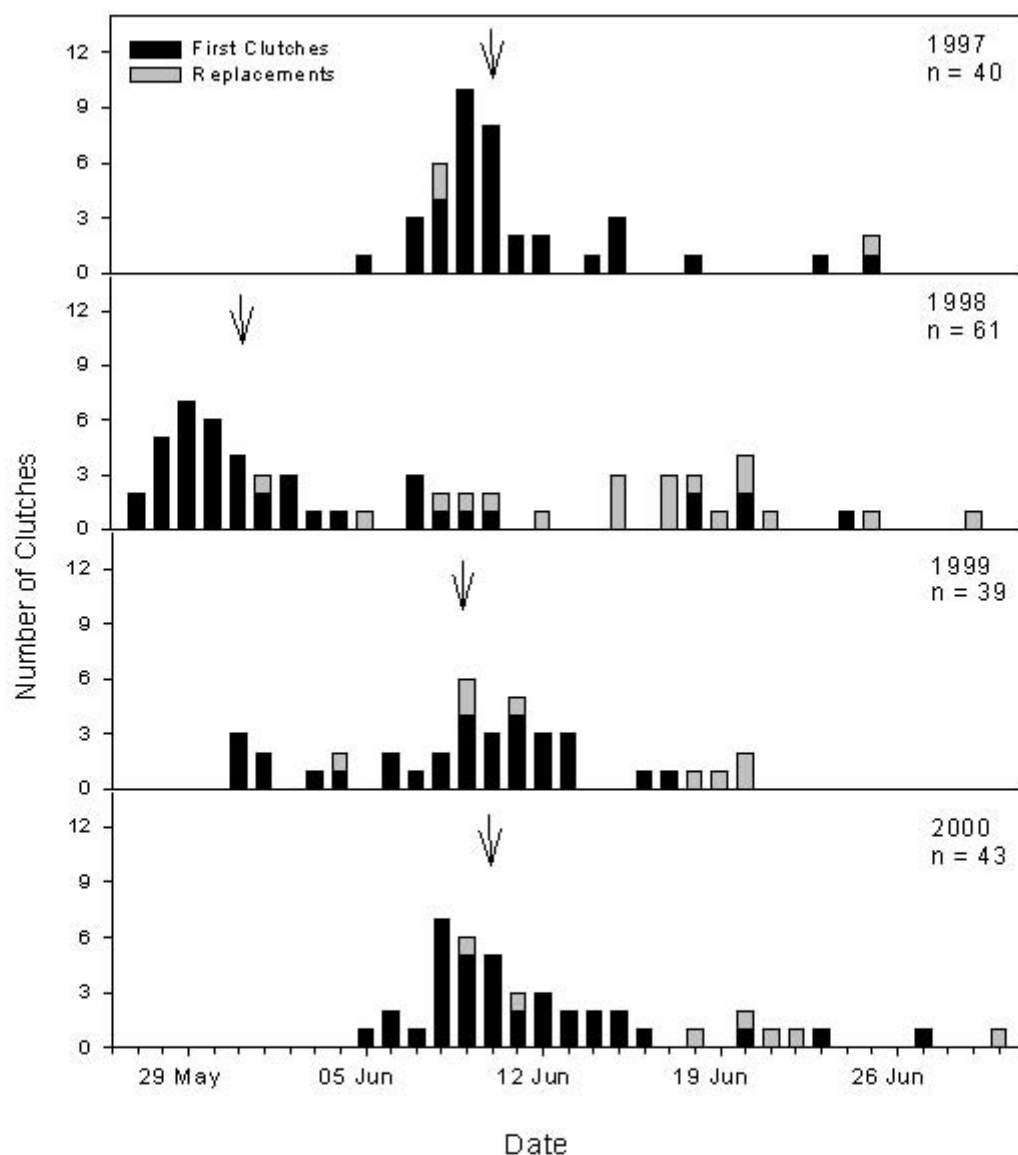
FIGURE 1.3 Clutch initiation dates of Yellow Warblers nesting on the study plot at Canvasback Lake, Alaska, 1997-2000. The arrow indicates the median initiation date of first clutches.
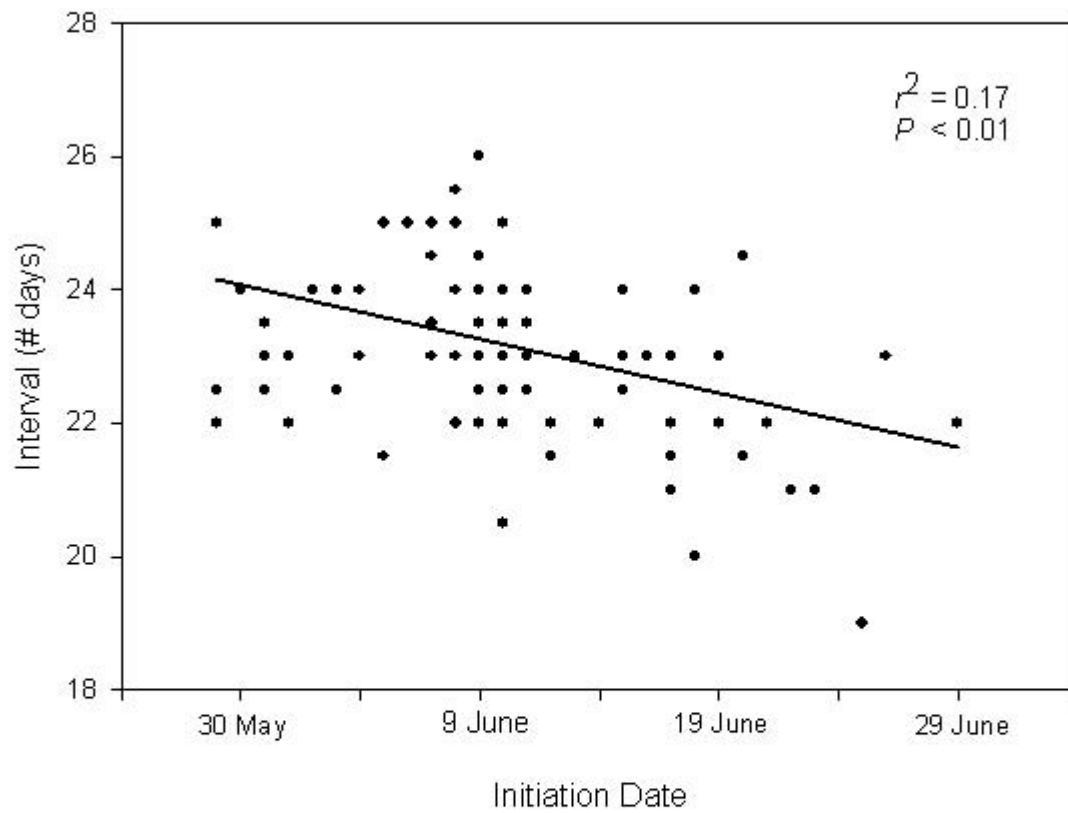
FIGURE 1.4. Relationship between duration of nesting interval and clutch initiation date for Yellow Warblers at Canvasback Lake, Alaska, 1997-2000. The regression model for this relationship was nesting interval = 36.9 - 0.08 * initiation date.
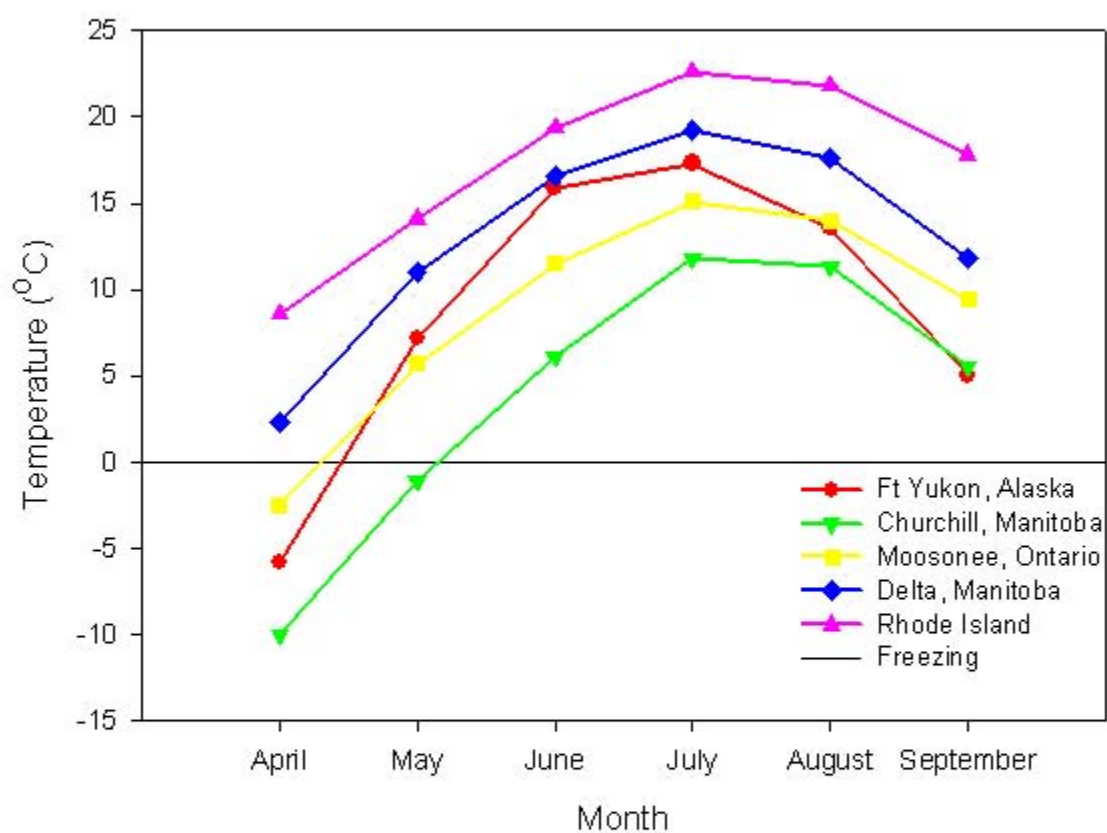
FIGURE 1.5. Temperature normals at weather stations close to sites where Yellow Warbler studies have been conducted. Data are from the Western Regional Climate Center and Environment Canada.

TABLE 1.1. Comparison of spring migration dates at Fairbanks, Alaska and initiation dates of first clutches at Canvasback Lake, Alaska for Yellow Warblers.

		Spring Migration Date[a]			Clutch Initiation Date	
Year	n	Median	Range	n	Median	Range
1997	10	2 June	31 May - 2 June	37	10 June	5 - 25 June
1998	13	25 May	20 - 31 May	42	31 May	27 May - 24 June
1999	6	30 May	26 May - 10 June	31	9 June	31 May - 17 June
2000	11	8 June	8 - 11 June	36	10 June	5 - 27 June

[a] Unpublished data courtesy of Alaska Bird Observatory, Fairbanks, Alaska.

TABLE 1.2. Comparison of distributions of clutch initiation dates among years. Results of Kolmogorov-Smirnov two-sample tests. Shows asymptotic K-S statistic with *P*-value in parentheses. After Bonferroni adjustment, only a *P*-value < 0.008 was significant.

	1998	1999	2000
1997	2.54 (< 0.001)	1.24 (0.09)	0.85 (0.46)
1998		2.96 (< 0.001)	3.36 (< 0.001)
1999			0.98 (0.29)

TABLE 1.3. Results of ANCOVA relating nesting interval to year and initiation date for Yellow Warblers at Canvasback Lake, Alaska, 1997-2000.

Variable	df	F	P
Model	51	1.70	0.04
Initiation Date	28	2.42	< 0.01
Year	3	1.72	0.18
Initiation Date x Year	20	1.01	0.47

TABLE 1.4. Timing of clutch initiation for Yellow Warblers breeding at several locations.

Location	n	Earliest	Latest	Author
Central Alaska	227	27 May	30 June	This study
Northern Manitoba	62	14 June	10 July	Briskie 1995
Northern Ontario	32	11 June[a]	28 June[a]	Rimmer 1988
Southern Manitoba	357	26 May	7 July	Goossen and Sealy 1982
Rhode Island	55	14 May	14 June	Mitra 1999

[a] Calculated from clutch completion dates and assuming a clutch size of 5 eggs.

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CHAPTER 2. REPRODUCTIVE SUCCESS OF THE YELLOW WARBLER IN A NORTHERN BOREAL FOREST WETLAND[2]

ABSTRACT. I studied the reproductive performance of Yellow Warblers (*Dendroica petechia*) in east central Alaska, monitoring 174 breeding pairs on Plot 1 in 1997-2000 and 39 pairs on Plot 2 in 1999. Nests were located in both willow shrub and spruce forest habitats, but breeding density was greater in willow. Clutch size ranged from 3-6 eggs; it did not differ significantly between habitats or among years, but declined seasonally. Partial loss of a clutch or brood was uncommon, but 7% of eggs that survived incubation did not hatch. Nest success did not vary seasonally, but differed among years and between habitats and plots. On Plot 1, nests on the edge between willow and spruce habitats were twice as likely to fail as those elsewhere in the plot. Predation was the probable cause of most nest failures. Successful pairs raised only one brood per season, but replacement of failed clutches or broods accounted for 20% of annual productivity. Estimated productivity per female was 2-3 fledglings on Plot 1 in 1997-2000 and <1 fledgling on Plot 2 in 1999. Estimated annual productivity per habitat on Plot 1 was 22 fledglings/ha in willow shrub and six fledglings/ha in spruce forest.

Key words: *annual productivity, breeding density, clutch size,* Dendroica petechia*, nest predation, nest success, Yellow Warbler*

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INTRODUCTION

Migratory passerines, particularly those that migrate between the Neotropical and Neararctic regions, travel tremendous distances and encounter diverse habitats and ecological conditions during their annual cycle. Population size and trends for these species may be influenced by events or conditions at their breeding areas, during migration, or at their wintering areas (Sherry and Holmes 1993, 1995). Detailed demographic information needed to understand what factors might affect the population dynamics of passerine species has been scarce (Askins et al. 1990, Martin 1992, Sherry and Holmes 1995). Because these factors will vary by species, habitat, region, and time of year, information is needed from a variety of populations (Sherry and Holmes 1995).

Several studies of migratory passerines have found a positive relationship between the number of adults captured in mist nets in one year and the number of hatching-year birds captured during the previous year, indicating that breeding productivity at these sites is an important determinant of variation in population size (Johnson and Geupel 1996, Chase et al. 1997, Gardali et al. 2000). Factors influencing productivity include age of breeding females (Nol and Smith 1987, Sanz 1995), weather conditions (Morton et al. 1972, Hejl et al. 1988), food availability (Martin 1987, Rodenhouse and Holmes 1992), quality of habitat (Andrén 1990) or territory (Petit and Petit 1996), rates of nest predation (Ricklefs 1969, Martin 1992), brood parasitism (Weatherhead 1989), and the duration of the breeding season (Morton 1976). Quantitative data are needed about the breeding ecology and reproductive success of

migratory passerines to evaluate the relationship between breeding season events and population dynamics.

Reproductive success is frequently estimated by the proportion of nests that produce one or more fledglings (nest success), the number of fledglings produced per nest, or the number of fledglings produced per female each season (annual productivity). Nest success and fledglings per nest are incomplete measures of reproductive success, because they do not account for multiple breeding attempts (Ricklefs and Bloom 1977, Underwood and Roth 2002). Production of multiple broods or replacement of lost clutches or broods increases the productivity of individuals and can enhance productivity of the population as a whole (Petrinovich and Patterson 1983, Holmes et al. 1992). Annual productivity is the most meaningful measure of reproductive success, but it is a difficult parameter to measure, because it involves tracking the success of individual females. Alternatively, annual productivity can be estimated indirectly from several reproductive parameters including clutch size, individual egg or nestling success, nest success, and the number of breeding attempts per female per season (Ricklefs and Bloom 1977, Murray 1991).

The Yellow Warbler (*Dendroica petechia*) is one of the most widespread and abundant species of warblers in the North America, breeding as far north as the Brooks Range in Alaska (Kessel and Gibson 1978) and as far south as New Mexico and northern Georgia (Dunn and Garrett 1997). This species inhabits a wide variety of deciduous woodlands and shrub-dominated habitats (Dunn and Garrett 1997), feeding on a diversity of insects and other arthropods (Busby and Sealy 1979). Although the

Yellow Warbler is a relatively well-studied species (see review in Lowther et al. 1999),

surprisingly little information is available for its annual productivity. Most studies

report information on clutch size and the success of individual nests rather than the

number of fledglings produced per female annually (Goossen and Sealy 1982, Mitra

1999), and older studies were limited by small sample sizes (Schrantz 1943, Young

1949, Batts 1961).

The purpose of the current study was to document the breeding biology and

assess the reproductive success of a population of Yellow Warblers nesting in a forest-

wetland mosaic in east central Alaska. Passerine populations nesting in central Alaska

have experienced few, if any, human-caused changes on their breeding grounds, are

free from the effects of brood parasitism by the Brown-headed Cowbird (*Molothrus

ater*), and are beyond the range of some of the nest predators that are important at lower

latitudes, such as raccoons (*Procyon lotor*) or snakes (Heske et al. 2001). In this study,

I examined various reproductive parameters for a partially marked population of

Yellow Warblers, including the number of breeding attempts per season, clutch size,

success of individual eggs, brood size, nest success, and the mean annual productivity

per female. I also investigated temporal and spatial variation in clutch size, nest

success, and productivity.

METHODS

STUDY AREA

During 1997-2000, I studied the breeding biology and reproductive success of Yellow Warblers at Canvasback Lake (66° 23'N, 146° 23'W) on the Yukon Flats National Wildlife Refuge in east central Alaska. Canvasback Lake is a 380-ha wetland that is rich in dissolved nutrients and highly productive, supporting a large biomass of aquatic invertebrates (Heglund 1988, Heglund, unpubl. data). Periodic flooding, a high frequency of wildland fires, and a discontinuous permafrost layer maintain a mosaic of boreal and wetland habitats in this region (Johnson and Vogel 1966). The predominant habitats at my study site included mature white spruce forest (*Picea glauca*) with scattered quaking aspen (*Populus tremuloides*), willow shrub thickets (a mixture of *Salix monticola*, *S. planifolia*, *S. arbusculoides*, *S. glauca*, *S. bebbiana*, *S. brachycarpa*, and *S. alaxensis*), graminoid meadows (dominated either by *Carex* spp. or by *Calamagrostis canadensis* and other grasses), and wet marshes (*Carex rostrata*, *C. aquatilis*, *Equisetum fluviatile*, or *Scirpus validus*). More than 30 species of passerines have been recorded as breeding near the lake, including the locally abundant Yellow Warbler (KMS, unpubl. data). Other common breeders included Yellow-rumped Warbler (*Dendroica coronata*), American Robin (*Turdus migratorius*), Western Wood-pewee (*Contopus sordidulus*), and Swainson's Thrush (*Catharus ustulatus*).

The Yukon Flats region has a subarctic, continental climate that is characterized by extreme seasonal variations in air temperature and day length. During the summer,

warm temperatures and long days produce an intense flush of vegetative growth and a rapid increase of insect biomass (U. S. Department of Interior, 1974). At Fort Yukon, which is approximately 55 km northeast of Canvasback Lake, the average daily minimum temperature exceeds 0°C from 14 May through 16 September (Western Regional Climate Center, 1961-1990). Continuous daylight with illumination exceeding civil twilight occurs from 10 May through 2 August (U. S. Naval Observatory 2001).

DATA COLLECTION

Nest Searching. I established one primary study plot, Plot 1 (12 ha), on the west shore of Canvasback Lake in 1997. A secondary plot, Plot 2 (15 ha), was set up on the south shore of the lake in 1998 but was searched intensively only in 1999 because of personnel constraints. The study plots were marked at 25-m intervals to provide a grid for systematic nest searching and a reference for mapping nests. My field assistants and I conducted intensive nest searches once or twice each week between late May and mid-July each year. Following Martin and Geupel (1993), nests were found by observing adult behavior and by visual searches of potential nest substrates. After nesting was complete, we measured nest locations in relation to the nearest grid point on the plot and marked these locations on a map (scale = 1 mm:1.6 m).

Color Marking. Staff of the Yukon Flats National Wildlife Refuge captured Yellow Warblers in mist nets on Plot 1 as part of an on-going mark-recapture study (permit # 22447) using the protocol of the Monitoring Avian Productivity and

Survivorship (M.A.P.S.) program (Burton and DeSante 1998). Sampling was conducted between 10 June and 1 August. I color banded adult Yellow Warblers that had a swollen cloacal protuberance or highly vascularized brood patch using a unique combination of colored leg bands that was randomly assigned to each individual. I conducted additional localized mist netting during May and June of 1998 and 1999 to increase the number of individually marked Yellow Warblers. Because I wanted to minimize disturbance at the nest sites and prevent premature fledging, I did not handle or band any nestlings.

Habitat. Habitats on the study plots were grouped into three broad categories based on the dominant canopy species: white spruce forest, willow shrub thicket, or graminoid meadow. I mapped the boundaries between habitats by walking between points on the 25-m grid and marking the habitat transitions on the map of the study plot. The area of each habitat was estimated from the maps using the mean of three measurements taken with a digital planimeter. Standard errors of area measurements were considerably underestimated, because the amount of error that occurred in creating the maps was not measured. I arbitrarily designated a strip 25 m in width between willow shrub thicket and spruce forest as willow-spruce edge. A nest was considered to occur on this edge if it occurred within this strip. I defined an open habitat edge as occurring between shrub or forest habitat and a meadow or lake and closed habitat edge as the border between willow shrub and spruce forest. I estimated the density of breeding pairs in each habitat by dividing the number of first breeding attempts by the estimated area of each habitat.

Nest Monitoring. My field assistants and I monitored nests every 3-5 days to provide information on nesting chronology and productivity. Signs of an active nest included observations of eggs or young or the presence of adults at the nest, including females incubating or brooding nestlings, adults feeding nestlings or removing fecal sacs, or adults defending the nest with alarm calls and injury-feigning displays. We used a mirror mounted on the end of a telescoping pole to examine the contents of nests that were less than 6 m above ground. Known clutch size was recorded if one of us observed the contents of a nest after laying was complete but before hatching had begun. I ascertained the timing of nesting activities either by direct observation or by backdating from known laying, hatching, or fledging dates. A nest was considered successful if one or more young fledged from it. If a nest failed, I continued to observe the behavior of the adults to determine if they replaced the failed nest.

Replacement nests were easily identified by the presence of color-banded adults, but many nesting adults were not color banded. I classified additional nests as replacements by the following criteria: (1) the distance between nests was $\leq$ 20 m or both nests were on the same breeding territory and (2) the interval between failure of one nesting attempt and initiation of the other clutch was $\leq$ 7 days. Additionally, a female using the material from one nest to build another was assumed to have built both nests. The preceding criteria were consistent with observations of multiple breeding attempts of color-banded individuals.

DATA ANALYSIS

Nest Success. I calculated daily nest survival rates using the Mayfield method

(Mayfield 1961, 1975). Nests entered into the analysis either on the day they were

found (eggs already present) or on the day the first egg was laid. I used the rules of the

"Last Active-B" method described by Manolis et al. (2000) to terminate the number of

days a nest was under observation. Nesting attempts that failed before laying or for

which the initiation date could not be determined were excluded from analysis.

Standard errors and confidence intervals for the Mayfield estimates were calculated

according to Johnson (1979). I used a weighted mean of the yearly survival rates, with

the number of exposure days as the weighting factor, to calculate the overall nesting

success over four years of this study (Johnson 1979).

I compared daily survival rates across nesting stages (laying, incubation, and

nestling), among years, and between habitats or plots using CONTRAST, a program for

comparing survival rates using χ^2 test statistics (Hines and Sauer 1989). Mayfield

survival rates for the entire nesting interval were calculated using 22 days, the average

duration of nesting for Yellow Warblers at Canvasback Lake (4 days for laying the first

4 eggs of a typical 5-egg clutch, 9 days for incubation, and 9 days for the nestling

period). I used the Bonferroni method to adjust the α levels for unplanned pairwise

comparisons. Unless noted otherwise, I did not compare Mayfield estimates if the

sample size was less than 20, the minimal size recommended by Hensler and Nichols

(1981).

I used proportional hazards regression (see Manolis et al. 2000) to test the effects of covariates (plot, year, clutch initiation date, habitat, open habitat edge, closed habitat edge) on nest success (PROC PHREG procedure in SAS; see Allison 1995). Unlike the Mayfield method, this procedure does not assume that nest success is constant through time and can be used to test continuous covariates. A nest began its exposure to the risk of failure on the day the first egg was laid; if a nest was found after the first egg was laid (left truncation), it entered into the analysis at a known age (Allison 1995: 161). A stepwise selection procedure was used to select the best model. Variables entered into the model with a significance of $P < 0.15$ and were retained at a significance level of $P < 0.10$. I used the "ties exact" option for dealing with tied nest failure dates, and I created indicator variables for categorical variables.

Annual Productivity. Because I had limited information on the exact number of young that fledged from each nest and only a portion of the study population was marked, I was unable to determine annual productivity through direct observation. Instead, I estimated productivity per female using two different methods. One estimate, designated as nestlings/female, was determined from brood sizes of the final nesting attempt per female per year. If all breeding attempts of a female failed in a given year, then that female produced zero fledglings that year. If a female had a successful breeding attempt, I assumed all nestlings from that nest successfully fledged. In some cases, the exact number of nestlings in a nest was difficult to determine because older siblings were covering younger siblings or I could not examine the brood too closely because the risk of triggering premature fledging was too high. If the exact number of

nestlings in a nest was uncertain (e.g., recorded as 4-5 young in nest), the minimum brood size was used to estimate productivity. I averaged all values in a given year to obtain the mean productivity per female per year.

A second estimate, designated as fledglings/female, was calculated for each year from the product of the following breeding parameters: mean clutch size, egg viability (the percent of the eggs that survived incubation that successfully produced nestlings), Mayfield estimates of nest success, and the number of breeding attempts per female per year (see Ricklefs and Bloom 1977, Murray 1991). I assumed that all females present at the study site attempted to breed and that I found at least one nest per female. Nests that failed before eggs could be laid were not included in the calculations.

Statistical Analyses. Statistical analyses were performed using the SAS statistical package, version 8.2 (SAS Institute 2001). Non-parametric methods were used for statistical analysis if assumptions of normality or equal variances were violated. Comparisons among years were restricted to Plot 1, while comparisons between plots were restricted to 1999. I examined variation in mean clutch size among years and between habitats using analysis of covariance (ANCOVA) with general linear models and type III sums of squares, including clutch initiation date as a covariate. I used linear regression models to examine the relationship between predicted clutch size and initiation date. I examined variation among years and between habitats in the number of nestlings/female using a Kruskal-Wallis test, with the Tukey test for *post hoc* multiple comparisons. I used the Mann-Whitney test to compare nestling productivity between study plots in 1999. I compared fledglings/female among years and between

habitats using χ^2 test statistics in Program CONTRAST (Hines and Sauer 1989). I examined the relationship between annual productivity in one year and breeding density in the following year using the Pearson product-moment correlation coefficient. Estimates of errors are standard errors (SE), and the significance level for all tests was $P < 0.05$ unless stated otherwise. Standard errors of estimated parameters, like breeding density and fledglings/pair, were obtained using the delta method (Oehlert 1992). Sample sizes differ among analyses because complete information was not available for every nest.

RESULTS

I monitored 215 nests and 174 breeding pairs on Plot 1 in 1997-2000 and 43 nests and 39 pairs on Plot 2 in 1999 (Table 2.1). Additionally, 14 nests were monitored on the west side of Plot 2 in 1998. Most nests (69%) were found during the nest building or egg laying stages, but a few nests (1%) were not found until one or two days before fledging and 5% of the nests were not found until after they had already failed. Multiple observations of color-banded adults were used to associate individuals with specific nests, mates, and fledglings. On Plot 1, color-banded males were observed at 48% of the nests, while color-banded females were observed at 27% of the nests. No individuals were banded on Plot 2, but two females and one male that had been color banded previously on Plot 1 nested on Plot 2.

BREEDING DENSITY AND HABITAT USE

The study plots included a mosaic of forest, shrub, meadow, and wetland habitats with a high proportion of edge habitat (Appendix 2.1). Willow-spruce edge, graminoid meadow, willow shrub thicket, and spruce forest accounted for 28%, 26%, 23%, and 22% of Plot 1, respectively (Fig. 2.1). On Plot 2, nearly half (49%) of the plot was covered by spruce forest; willow-spruce edge, willow shrub thicket, and graminoid meadow comprised 24%, 16%, and 11% of the plot, respectively. The mean density of breeding pairs on Plot 1 was 3.6 ± 0.01 pairs/ha in 1997-2000, while the breeding density on Plot 2 in 1999 was 2.7 ± 0.01 pairs/ha.

Yellow Warbler nests were not equally distributed among habitats. Breeding density was substantially greater in willow shrub habitat than in the other habitats on both study plots (Table 2.2). Willow-spruce edge habitat was settled at a slightly lower density, on average, than spruce forest on Plot 1 in 1997-2000 but was settled at a much higher density than spruce forest on Plot 2 in 1999. No nests were found in graminoid meadows or wet marshes, probably because of the lack of woody nesting substrates. Nesting substrates included willow shrubs ($n = 219$), white spruce trees ($n = 46$), and deciduous trees ($n = 7$), including paper birch (*Betula papyrifera*), balsam poplar (*Populus balsamifera*), and quaking aspen. On Plot 1, the number of breeding pairs that nested in willow shrub and willow-spruce edge was relatively consistent among years (Table 2.2). In 1998, however, nearly twice as many pairs nested in spruce forest on Plot 1 than in the other three years.

CLUTCH AND BROOD SIZE

Clutch size ranged from 3-6 eggs with a mean of 4.8 ± 0.1 for all breeding attempts (Table 2.1). In each year, clutch size declined significantly as the season progressed (Fig. 2.2). I examined variation in mean clutch size among years and between habitats on Plot 1 using ANCOVA. Neither habitat nor the interaction between habitat and initiation date had a significant impact on clutch size and both variables were removed from the model (Table 2.3). In the reduced model, I did not detect a significant difference in mean clutch size among years, but the interaction between initiation date and year was significant and influenced the analysis (Table 2.3 and Fig. 2.2). Some females replaced breeding attempts that failed. Replacement clutches were smaller (mode = 4 eggs; 20 of 35 clutches) than first clutches (mode = 5 eggs; 72 of 120 clutches).

Successful females raised only one brood per season. Known brood size within two days of fledging ranged from 2-6 young with a mean of 4.4 ± 0.2 for all breeding attempts ($n = 36$). Not all eggs laid in a clutch were viable; nearly 4% of 428 eggs laid in 89 nests that survived until hatching did not hatch. In almost all cases, hatching failure affected only a single egg in a clutch. Additionally, some nestlings apparently died during the hatching process or shortly thereafter and were absent from the nest when it was first observed after hatching. For 70 clutches in which both clutch size and post-hatching brood size were known (42% of all clutches that survived until hatching), 93% of eggs laid produced viable nestlings.

NEST SUCCESS

At least one young fledged from 45% (96 of 215 nests) of the nests on Plot 1 and 16% (9 of 57 nests) of the nests on Plot 2. Fledging was assumed if fledglings were observed near the nest, an adult was carrying food or giving alarm calls near an empty nest at the time fledging was expected to have occurred, or nestlings were at least eight days old when the nest was last checked. A total of 141 nests failed to produce any fledglings. Failures were inferred from the disappearance of nest contents before the earliest expected fledging date, damage of the nest or nest lining, observation of a female dismantling one nest to build another, the presence of egg shell pieces or dead young, or the lack of adult activity at a nest before expected fledging (Table 2.4). I could not determine the fate of 26 nests.

Proportional hazards regression was used to examine the effect of clutch initiation date, year, and plot on nest success. The best model included the variables for plot and the year 1998 (Table 2.5). Nests were more than three times as likely to fail on Plot 2, at least in 1999, as on Plot 1. Nests were also twice as likely to fail in 1998 as in the other three years. The timing of clutch initiation did not have a significant impact on nest success.

I calculated the percentage of nests that failed in relation to the number of nests that were active and at risk of failure for each consecutive 5-day period starting on the day the first egg was laid in a season (Fig. 2.3). In three of the years (1997, 1998, and 2000), percent loss of nests was greatest during the period that had the greatest number of active nests. In 1999, however, the greatest proportion of nest failures on both study

plots occurred later in the nesting period, when the number of nests at risk was decreasing.

Mayfield estimates of nest success were calculated using the daily survival probability for the entire nesting period (from first egg to fledging of first young), because daily survival rates of nests did not differ significantly among the laying, incubation, and nestling stages within any year except 1997 (1997: $\chi^2 = 10.21$, $P < 0.01$; 1998: $\chi^2 = 4.23$, $P = 0.12$; 1999, Plot 1: $\chi^2 = 4.73$, $P < 0.10$; 1999, Plot 2: $\chi^2 = 4.60$, $P = 0.10$; 2000: $\chi^2 = 0.65$, $P = 0.72$). Because of the small sample sizes for replacement clutches, nest success was not calculated separately for first and replacement clutches. Daily nest survival rates were not homogeneous among years ($\chi^2 = 11.01$, $P = 0.01$) or between study plots (1999 only; $\chi^2 = 10.40$, $P < 0.01$; Table 2.6). Nest success was lower in 1998 than in the other three years, but this difference was significant only between 1997 and 1998 ($\chi^2 = 9.92$, $P < 0.01$). In 1999, nest success was very low on Plot 2, less than half of that on Plot 1 (Table 2.6).

REPRODUCTIVE SUCCESS AND HABITAT

Finally, I examined habitat-related differences in reproductive success. First, I compared clutch sizes between willow shrub and spruce forest. For this analysis, I ignored the edge zone and classified nests by the dominant habitat type that occurred at each nest site. Although mean clutch size appeared to be smaller in spruce forest than in willow shrub (Table 2.7), I did not detect a significant effect of habitat on clutch size (see full model in Table 2.3). There was considerable overlap of the 95% confidence

intervals for predicted clutch sizes obtained from the linear regression analysis relating clutch size to initiation date for the two habitats (Fig. 2.6). The contents of nests located in spruce trees were often difficult to observe because of greater nest heights and the relatively high density of overhanging cover. Consequently, the power to detect differences between habitats was affected by the limited number of known clutch sizes in spruce forest.

I used proportional hazards regression to examine the effect of habitat (spruce forest or willow shrub) and habitat edge (yes or no) on nest success for nests found on Plot 1. Two types of edge variables, closed edge and open edge, were included in the analysis. Since nest success was significantly lower in 1998 than in the other three years, the variable for this year was also entered in the analysis. The best model included the variables for year 1998, willow-spruce edge, and habitat (Table 2.5). The effect of habitat was only marginally significant.

I calculated Mayfield estimates of nest success for each habitat on Plots 1 and 2 (Table 2.6). Sample sizes were too small (most < 20) to obtain reliable Mayfield estimates of nest success in spruce habitat for a given year, so I did not conduct within-year comparisons. Nest success, pooled across years, was significantly higher in willow habitat than in spruce forest ($\chi^2 = 4.86$, $P < 0.03$). Nest success also differed between similar habitats in different locations. In 1999, the daily survival rate of nests in willow habitat was significantly lower on Plot 2 than on Plot 1 ($\chi^2 = 10.89$, $P < 0.01$).

ANNUAL PRODUCTIVITY

At least 52% of the pairs that nested on Plot 1 during the four years of the study successfully produced fledglings. Most of these pairs fledged young during a single breeding attempt, but 15 breeding pairs (9% of total) did not produce fledglings until their second attempt and one pair fledged young during a third attempt. In 14% of the pairs, it was unknown if they produced any young. Most pairings were monogamous, but polygyny was observed in 3 out of 174 pairings (< 2%) on Plot 1. Polygyny did not enhance the reproductive success of these three males, because only the nesting attempt that received more attention from the male was successful.

On Plot 1, annual productivity ranged from 2-3 young per female (Table 2.1). The mean number of nestlings/female did not differ significantly from estimates of fledglings/female within any year (1997: $\chi^2 = 0.03$, $P = 0.86$; 1998: $\chi^2 = 0.20$, $P = 0.65$; 1999: $\chi^2 = 0.88$, $P = 0.35$; 2000: $\chi^2 = 1.20$, $P = 0.27$; Fig. 2.4). I compared mean number of nestlings/female across years ($H_3 = 3.89$, $P = 0.01$), but nestlings/female differed significantly only between 1997 and 1998 ($P < 0.05$). The estimated number of fledglings/female also differed significantly only between 1997 and 1998 ($\chi^2 = 12.50$, $P < 0.001$). Breeding density in a particular year appeared to be positively related to productivity per female of the preceding year, at least for mean nestlings/female (nestlings/female: $r = 1.0$, $P < 0.04$; fledglings/female: $r = 0.93$, $P = 0.25$; Fig. 2.5); however, small sample size and large confidence intervals prevented a robust test of this working hypothesis (Fig. 2.5).

On Plot 2, annual productivity was very low (< 1 young per female) in 1999 (Table 2.1). The mean number of nestlings/female did not differ significantly from estimated fledglings/female ($\chi^2 = 0.45$, $P = 0.50$). Young produced per female on Plot 2 differed significantly from young per female on Plot 1 in 1999 (nestlings/female: $Z = 3.87$, $P < 0.001$; fledglings/female: $\chi^2 = 10.76$, $P < 0.01$; Fig. 2.4).

I compared annual productivity between willow shrub and spruce forest (Table 2.7). Across the four years of the study, the mean number of nestlings/female on Plot 1 was greater in willow shrub than in spruce forest ($H_{1,3} = 2.49$, habitat: $P = 0.03$, year: $P = 0.02$, year x habitat: $P = 0.68$). The estimated number of fledglings/female on Plot 1, pooled across years, was also significantly greater in willow habitat than spruce forest ($\chi^2 = 5.15$, $P < 0.03$). Within each year, I did not detect a significant difference in nestlings/female or fledglings/female between habitats ($P > 0.10$ for each pair). Yellow Warblers on Plot 1 produced approximately 19.2 ± 1.0 nestlings/ha or 22.2 ± 1.8 fledglings/ha in willow shrub habitat and 6.7 ± 0.6 nestlings/ha or 6.3 ± 0.7 fledglings/ha in spruce forest annually.

DISCUSSION

BREEDING DENSITY AND HABITAT USE

Breeding densities of Yellow Warblers observed at various locations in North America have been highly variable, probably a reflection of the variety of habitats used by this species (Table 2.8). Across their geographic range, Yellow Warblers nest in wet shrub thickets, river and lake margins, floodplains, swamps and bogs, deciduous woodlands,

gardens, overgrown fields and pastures, forest edges, and other shrub-dominated habitats (Bent 1953, Schroeder 1982, Graber et al. 1983, Peck and James 1987). Overall breeding densities on the study plots at Canvasback Lake were comparable to the mid-range densities observed in southeast Ontario (Yezerinac et al. 1999) and southern Wisconsin (Young 1949). In comparison to other areas, breeding densities at the study site were high (> 6 pairs/ha) in willow shrub habitat and moderate (3.5-4.5 pairs/ha) in willow-spruce edge habitat. On Plot 1, the average density of breeding pairs in spruce forest was comparable to densities in shrubby habitats in other areas. It is unusual for Yellow Warblers to occupy coniferous habitats or use conifers as nesting substrates (see Hebard 1961, Morse 1973, Peck and James 1987, Brooks 1993), but 25% of the pairs on the study plots nested in spruce forest and almost 20% of the nests were constructed in spruce trees.

Two features of the study plots may have promoted the atypical use of spruce forest at Canvasback Lake -- proximity of shrub habitat and proximity of lakeshore. The study plots at Canvasback Lake included a mosaic of habitats, therefore, the spruce stands on the plots were relatively small and included a high proportion of edge in relation to interior (see Appendix 2.1). Perhaps Yellow Warblers occupied spruce forest because willow shrub habitat was nearby. Morse (1973) observed that Yellow Warblers occupied conifer-dominated islands off the coast of Maine, but they continued to conduct most of their foraging in adjacent deciduous habitats. The forest stand on Plot 2 was more than twice as large as that on Plot 1; the low breeding density in spruce forest on Plot 2 may have been a consequence of reduced willow shrub edge.

Proximity to lakeshore may also have been an important component of habitat quality at Canvasback Lake. LaRue et al. (1995) reported a higher abundance of breeding birds in riparian coniferous forest than in forest stands of similar vegetation structure and composition that were not near water. Riparian or lakeshore communities have a high abundance of food for insectivorous birds because of the presence of both aquatic and terrestrial invertebrates (Jackson and Fisher 1986, Gray 1993, Petit and Petit 1996). Yellow Warblers may have occupied spruce forest habitat because of the overriding benefit of being close to an abundant food resource.

CLUTCH AND BROOD SIZE

The typical clutch size for Yellow Warblers breeding in North America is 4 or 5 eggs (Goossen and Sealy 1982, Peck and James 1987, Briskie 1995, Mitra 1999). Reports of 6-egg clutches are rare (Schrantz 1943, Weatherhead 1989, Peck and James 1987). At Canvasback Lake, Yellow Warblers usually laid clutches of 4 or 5 eggs, but 14% of the clutches contained 6 eggs. Clutch size tends to increase with latitude for a number of avian species (Klomp 1970, Kulesza 1990, Briskie 1995). Several hypotheses have been proposed to explain this latitudinal gradient in clutch size. Food availability, an important factor limiting clutch size, is believed to be greater at higher latitudes (Lack 1954, Ashmole 1963). At Canvasback Lake, food resources appeared to be diverse and abundant, which may have allowed females in the study population to produce larger clutches, on average. Alternatively, Martin (1995) suggested that clutch size is influenced by a trade-off between the risk of nest predation and the length of the

breeding season (see also Farnsworth and Simons 2001). An abbreviated breeding season, such as that at Canvasback Lake, provides a constraint on the number of breeding attempts that can be initiated, which may provide selection for larger clutches. Selection for larger clutches is enhanced if nest predation rates are relatively low.

Clutch size did not differ substantially among the four years at Canvasback Lake, but did decrease as the season progressed. Many avian species experience a seasonal decline in clutch size (Klomp 1970, Bryant 1975, Nolan 1978, Hochachka 1990), including Yellow Warblers at other areas (Goossen and Sealy 1982, Mitra 1999). Many hypotheses have been proposed to explain this seasonal decline, including age-related differences in clutch size and laying date (Askenmo and Unga 1986, Hochachka 1990), seasonal decline in food availability (Perrins 1970, Murphy 1986), reduced investment of the female in later clutches because late offspring are less likely to survive their first year (Lack 1966, Nilsson and Smith 1988), or reduced overwinter survival of adults that invest considerably in reproduction late in the breeding season (Hussell 1972). The reduced probability that late-fledging young or late-breeding adults will survive is probably of greater importance in species with restricted breeding seasons.

Reduction in the size of a clutch or brood during a nesting attempt can decrease productivity of a breeding pair. Clutch or brood size may be reduced through poor egg viability (Koenig 1982, Hendricks and Norment 1994), failure of young to survive hatching (Nolan 1978), partial predation of a clutch or brood (Sealy 1994), starvation of nestlings (Orell and Ojanen 1983), or removal or damage of eggs or nestlings by brood

parasites (Scott et al. 1992). Mean brood size at Canvasback Lake was slightly smaller than clutch size, mostly a result of eggs that failed to hatch or young that failed to survive the hatching interval. At my study site, the percentage of eggs present at hatching time that produced viable nestlings was similar to average egg viability reported for other passerines (91%, n = 95 populations; Koenig 1982). Partial predation of a clutch or brood, starvation of nestlings, and brood parasitism were not important factors in clutch or brood reduction at my study site.

NEST SUCCESS

Numerous estimates of nest success for Yellow Warblers are in the published literature, but I was unable to conduct rigorous comparisons because many studies did not calculate Mayfield estimates or publish error estimates. For studies that included more than 20 nests in their estimates, nest success ranged from 29% in agricultural areas of western Montana (Tewksbury et al. 1998) to 65% in southeastern Alaska (Willson and Gende 2000; Table 2.9). Nest success on Plot 1 was about, or slightly above average, compared to other locations in North America. Similar percentages of nest success were observed at Delta Marsh and Churchill, Manitoba, the Sierra Nevada in California, and the Great Swamp in Rhode Island (Goossen and Sealy 1982, Weatherhead 1989, Briskie 1995, Mitra 1999, Cain et al. 2003). Nest success on Plot 2 in 1999 was extremely low and comparable to the estimate of success for nests parasitized by Brown-headed Cowbirds at Delta Marsh, Manitoba (Goossen and Sealy 1982).

Loss of an entire clutch or brood can occur as a result of severe weather (Morton et al. 1972, Murphy 1983, Bollman and Reyer 2001), poor food availability (Blancher and Robertson 1987, Holmes et al. 1991, Rotenberry and Wiens 1991), brood parasitism (Brittingham and Temple 1983, Budnik et al. 2000), or nest predation (Picman and Schriml 1994, Hoover et al. 1995, Hanski et al. 1996). I researched causes of nest failures for Yellow Warblers at other locations. Weather conditions and starvation of young resulted in the failure of some nests at other sites, but the proportion of failures from these causes was relatively minor (Goossen and Sealy 1982, DellaSala 1985, Weatherhead 1989, Briskie 1995, Cain et al. 2003). At my study site, weather conditions were generally moderate during the four years of the study and did not significantly impact nest success. Starvation of young was suspected at only two nests.

Brood parasitism by the Brown-headed Cowbird was a significant problem at many sites, including those with lower nest success than occurred on Plot 1 (Clark and Robertson 1979, DellaSala 1985, Peck and James 1987, Weatherhead 1989, Tewksbury et al. 1998), but the breeding range of the cowbird extends only as far north as southeast Alaska and northern British Columbia (Lowther 1993). Brood parasitism does not occur at Canvasback Lake and will not be considered further.

Nest predation was the primary cause of nest failures for Yellow Warblers at many sites, (Goossen and Sealy 1982, Briskie 1995, Hanski et al. 1996, Willson and Gende 2000, Cain et al. 2003) and is the most significant factor affecting nest success for many populations of passerines (Nice 1957, Ricklefs 1969, Martin 1992). Although

I witnessed only one act of predation on a Yellow Warbler nest, nest predation was the likely cause of most nest failures at my study site (see Table 2.4).

The two most likely nest predators at the study site were red squirrels (*Tamiasciurus hudsonicus*) and Gray Jays (*Perisoreus canadensis*). They were observed regularly throughout the season on both study plots. Both species are important nest predators in northern forests (Ouellet 1970, Darveau et al. 1997, Boulet et al. 2000). Other potential nest predators present at the study site included northern flying squirrel (*Glaucomys sabrinus*), pine marten (*Martes americana*), short-tailed weasel (*Mustela erminea*), mink (*Mustela vison*), least weasel (*Mustela nivalis*), red fox (*Vulpes vulpes*), black bear (*Ursus americanus*), voles (*Clethrionomys rutilus* and *Microtus* spp.), Common Raven (*Corvus corax*), Red-winged Blackbird (*Agelaius phoeniceus*), Mew Gull (*Larus canus*), Bonaparte's Gull (*Larus philadelphia*), Northern Hawk Owl (*Surnia ulula*), and Sharp-shinned Hawk (*Accipiter striatus*). Many of these species have been reported as nest predators in other studies (Kertell 1986, Andrén 1992, Joy et al. 1994, Picman and Schriml 1994, Hanski et al. 1996, Sieving and Willson 1998, and Farnsworth and Simons 2000).

Nest predation rates can vary seasonally, annually, and by location as changes occur in the availability of low-risk nest sites (Hartley and Shepherd 1994, Martin 1993), composition and behavior of the potential nest predator community (Sieving and Willson 1998, Sieving and Willson 1999, Petit and Petit 1996), density of available prey (Gates and Gysel 1978, Martin 1988, Pelech 1999), and availability of alternative prey for potential nest predators (Dunn 1977, Orell and Ojanen 1983, Schmidt and

Ostfeld 2003). I observed both temporal and spatial variation in nest success at Canvasback Lake. Temporal differences in nest success usually involved a specific year. In 1999, a greater proportion of nests failed later in the season than earlier in the summer, possibly in response to a seasonal change in predator abundance that did not occur in the other three years. A higher density of predators in 1998 compared to the other years may have been responsible for the lower nest success in that year. Additionally, predators may have been more successful at finding nests in 1998, particularly in spruce forest, because nesting density was higher in 1998 than in the other three years. Plot 2 was less than 1 km away from Plot 1, but nest survival rates were considerably different between the two plots. Sometimes, a local predator can make a considerable difference in nest success at a particular site (Petit and Petit 1996). In 1999, a pair of Northern Hawk Owls nesting on Plot 2 may have substantially reduced the nest success of Yellow Warblers on this plot.

REPRODUCTIVE SUCCESS AND HABITAT

During this study, I did not detect a significant difference in clutch size between habitats, but breeding habitat did affect nest success. Nest success can differ between habitats because of differences in the availability of food resources (Sanz 1995, Petit and Petit 1996), the quality of available nest sites (Alatalo et al. 1985, Martin 1993), the number and type of local predators (Patnode and White 1992, Heske et al. 2001), and the age composition of breeding adults (Petit and Petit 1996). At Canvasback Lake, the relative risk of nest predation in a particular habitat likely was an important component

of habitat-specific nest success. On Plot 1, two of the habitat features I examined likely had an impact on nest success: (1) the structure of the dominant canopy community (coniferous forest vs. deciduous shrub) and (2) the structural heterogeneity of the habitat (habitat interior vs. edge).

On Plot 1, nests located primarily in spruce forest were not as successful, on average, as those located primarily in willow shrub habitat. The significance of this relationship was marginal, possibly because edge effects diluted the differences between the two habitats, but I believe it was still important. The structure of the dominant plant species differed considerably between the two habitats. Yellow Warblers typically nest in deciduous shrub habitats, and individuals may not have been as adept at selecting low-risk nest sites in spruce forest. In addition, nest predator communities may have differed between the two habitats. For example, red squirrels, which are concentrated in coniferous forest habitats because of their dependence on conifer seeds as an winter food resource (Smith 1968), may have contributed to the lower nest success in spruce forest at Canvasback Lake. Several studies have observed that red squirrels are an important nest predator in coniferous forest habitats (Sieving and Willson 1998, Tewksbury et al. 1998, Rodewald and Yahner 2001). On Plot 2, nest success was lower in shrub habitat than in spruce forest, but hawk owls were frequently observed perched above willow shrub thickets and, as noted previously, may have been an important nest predator in this situation.

On Plot 1, nests located on the border between willow shrub and spruce forest habitats were twice as likely to fail as those elsewhere on the plot. Sometimes

predation rates are higher at habitat edges because prey densities are higher in comparison to adjacent habitats (Gates and Gysel 1978). Yellow Warbler breeding densities at the study site, however, were not higher on the willow-spruce edge than in the adjacent habitats. Alternatively, increased predation could have occurred at the transition zone between the two habitats because this edge was visited by predators from both habitats (Andrén 1995). In addition, some predators are more likely to forage along habitat edges (Wilcove 1985, Yahner and Scott 1988). All habitat edges are not equal; placement of a nest on an open edge adjacent to a meadow or lake did not have a significant impact on nest success at Canvasback Lake. The risk of predation for nests on habitat edges will vary depending on the type of edge, the landscape composition surrounding the edge, and the type of predators present (Andrén 1995).

ANNUAL PRODUCTIVITY

Directly observing the number of fledglings produced per female per year (annual productivity) is a difficult and labor intensive process that involves following individually marked birds throughout the season. One problem I encountered in determining annual productivity was the difficulty in determining exactly how many young were in the nest immediately prior to fledging. Nests with nestlings > 5 days old were very crowded. It was frequently difficult to determine the exact number of young in the nest, unless eyes or beaks were visible. Even then, larger siblings frequently covered smaller siblings. Older Yellow Warbler broods were also sensitive to disturbance, and it was easy to trigger premature fledgling by examining the nest too

closely (pers. obs.). Maximum brood size was not known in all cases, so the number of

nestlings/female was the minimum number of nestlings verified in the nest and

probably underestimated productivity per female.

I also estimated productivity per female from the product of four breeding

parameters: number of breeding attempts per female per season, mean clutch size, the

average proportion of eggs that survived hatching and produced viable young (egg

viability), and Mayfield nest success. Most of these breeding parameters were

relatively easy to obtain through field observations. The most difficult parameter to

obtain was the number of breeding attempts per female per season. Not all of the

breeders in my study population were individually marked. I used a combination of

direct observation of marked individuals and inferences drawn from the behavior of

these individuals to identify first breeding attempts and their replacements. Identifying

replacement nests is important, because replacement clutches can account for a

significant proportion of annual fledgling production (Martin 1982, Petrinovich and

Patterson 1983, Thompson et al. 2001). Using the criteria described in the methods, I

was conservative in classifying a nest as a replacement. Identifying a nest as a first

attempt rather than as a replacement could have decreased estimates of productivity per

female, but I believe most nests were classified correctly. Ricklefs and Bloom (1977)

developed a model that estimates annual productivity from several breeding parameters,

but they suggested using duration of the breeding season to estimate the number of

breeding attempts per female per season. Other models have also been developed to

estimate annual productivity (Murray 1991, and Pease and Grzybowki 1995). In my

study, the estimates of fledglings/female obtained from the four breeding parameters were similar to the estimates of nestlings female obtained from brood sizes.

Nest success was the most important factor limiting annual productivity of Yellow Warblers at my study site and was responsible for much of the spatial and temporal variation in reproductive success. Replacement of lost clutches or broods, however, was important for increasing productivity per female, particularly of females nesting in spruce habitat (compare nestlings/nest and nestlings/female in Tables 2.1 and 2.7). If multiple breeding attempts had not been considered, mean annual productivity over the four years of the study would have been underestimated by 0.5 fledglings/female. Although multiple brooding can also increase the productivity of individuals (Holmes et al. 1992), female Yellow Warblers breeding at Canvasback Lake raised only one brood per year. Several males attempted to raise more than one brood per year through polygynous matings, but were unsuccessful. Polygyny occurred at a low frequency, similar to other populations (Ford 1983, DellaSala 1986, Hobson and Sealy 1989), and probably had a very minor impact on annual productivity.

The Yellow Warblers nesting at my study site laid slightly larger clutches, on average, than those in many other areas. Larger clutch sizes could have resulted in greater numbers of fledglings produced per female compared to other areas with similar rates of nest success. Estimates of productivity per female for Yellow Warblers were not available in the literature, but a few studies reported the number of fledglings produced per nest. Yellow Warblers nesting in southern Manitoba produced 1.8 fledglings per nest for unparasitized nests (Goossen and Sealy 1982), which was

comparable to the average of 1.9 fledglings per nest on Plot 1 at Canvasback Lake.
Yellow Warblers in southeast Ontario also produced 1.8 fledglings per nest, but
fledgling production at this site was depressed by cowbird parasitism, which affected
41% of nests (Clark and Robertson 1979). Individuals breeding at these lower latitude
sites had longer breeding seasons than warblers at Canvasback Lake and presumably
had more opportunities for replacing lost clutches or broods, thereby increasing their
individual productivity. Therefore, per capita annual productivity does not appear to be
exceptional at Canvasback Lake in comparison to southern Manitoba and southeast
Ontario.

The annual productivity of populations is determined by the number of
fledglings produced per pair and the density of breeding pairs, both of which may be
highly variable in a landscape that includes a diversity of habitats of differing quality.
At Canvasback Lake, breeding densities and productivity varied among habitats.
Willow shrub habitat and spruce forest each comprised approximately 36% of the area
on Plot 1, but Yellow Warblers nesting in willow shrub annually produced an average
of 22 fledglings/ha, while those nesting in spruce forest produced only six fledglings/ha
each year. According to source-sink models of population dynamics (Pulliam 1988)
and habitat selection models of Fretwell and Lucas (1970), areas of good quality habitat
and high productivity (e.g., willow shrub) tend to produce surplus individuals that are
forced to emigrate or occupy poorer quality habitat that is nearby (e.g., coniferous
forest), because breeding sites are already occupied in the good quality habitat. On Plot
1, the differences between habitats in breeding density and reproductive success of

Yellow Warblers agree with source-sink models. Understanding the relationships between habitat use and reproductive success is important for studying population dynamics at a larger scale.

Because adult survival rates of migratory passerines tend to be relatively low (see DeSante and O'Grady 2000), annual productivity can have a significant impact on the size of the breeding population. Several studies have observed a positive relationship between density of breeding pairs and annual productivity of the preceding year (Nolan 1978, Holmes et al. 1992, Sherry and Holmes 1992), and this relationship appeared to occur at my site as well. Despite its importance for understanding population dynamics, relatively few estimates of annual productivity are available in the published literature for avian species (Thompson et al. 2001). Greater emphasis needs to be placed on estimating productivity per female rather than productivity per nest, more effort is needed to study the relationships between nest predator populations and nesting bird populations, and more detailed information is needed about factors that influence the productivity of individuals of various species in a variety of habitats and locations.
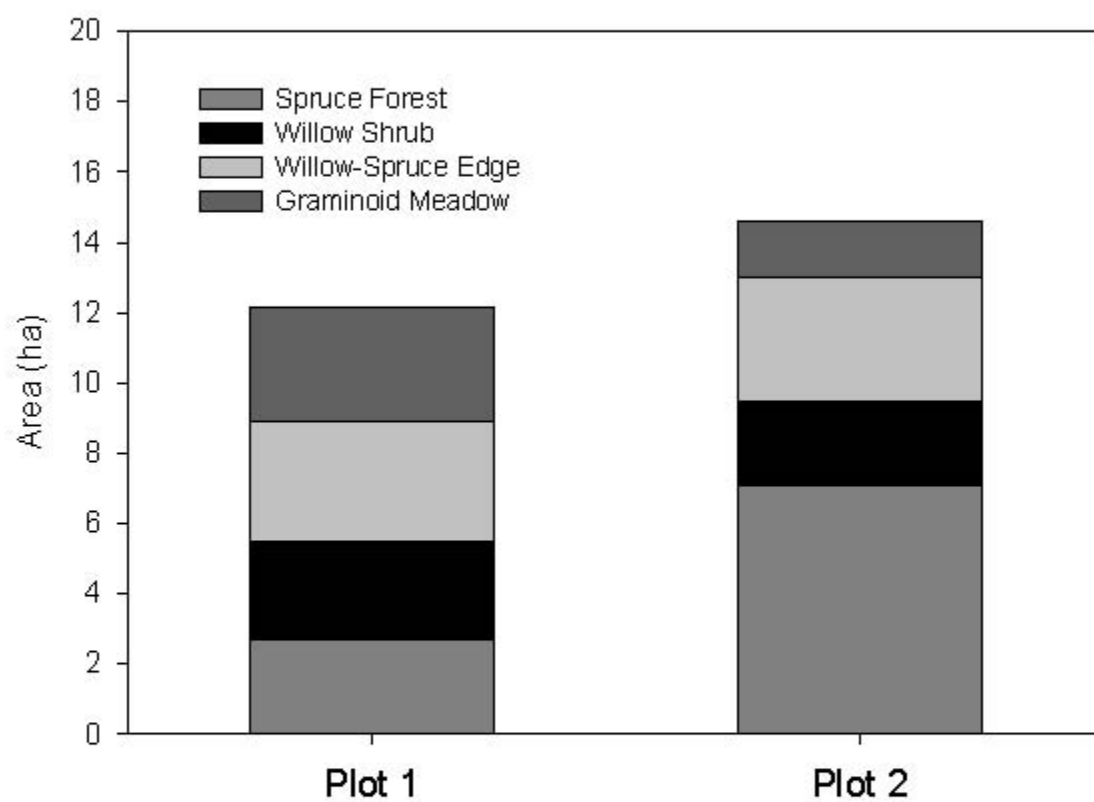
FIGURE 2.1. Relative areas of habitat types on the study plots at Canvasback Lake, Alaska, 1997-2000.

FIGURE 2.2. Relationship of clutch size to clutch initiation date and year for Yellow Warblers nesting on Plot 1 at Canvasback Lake, Alaska, 1997-2000. Results of linear regression analysis.
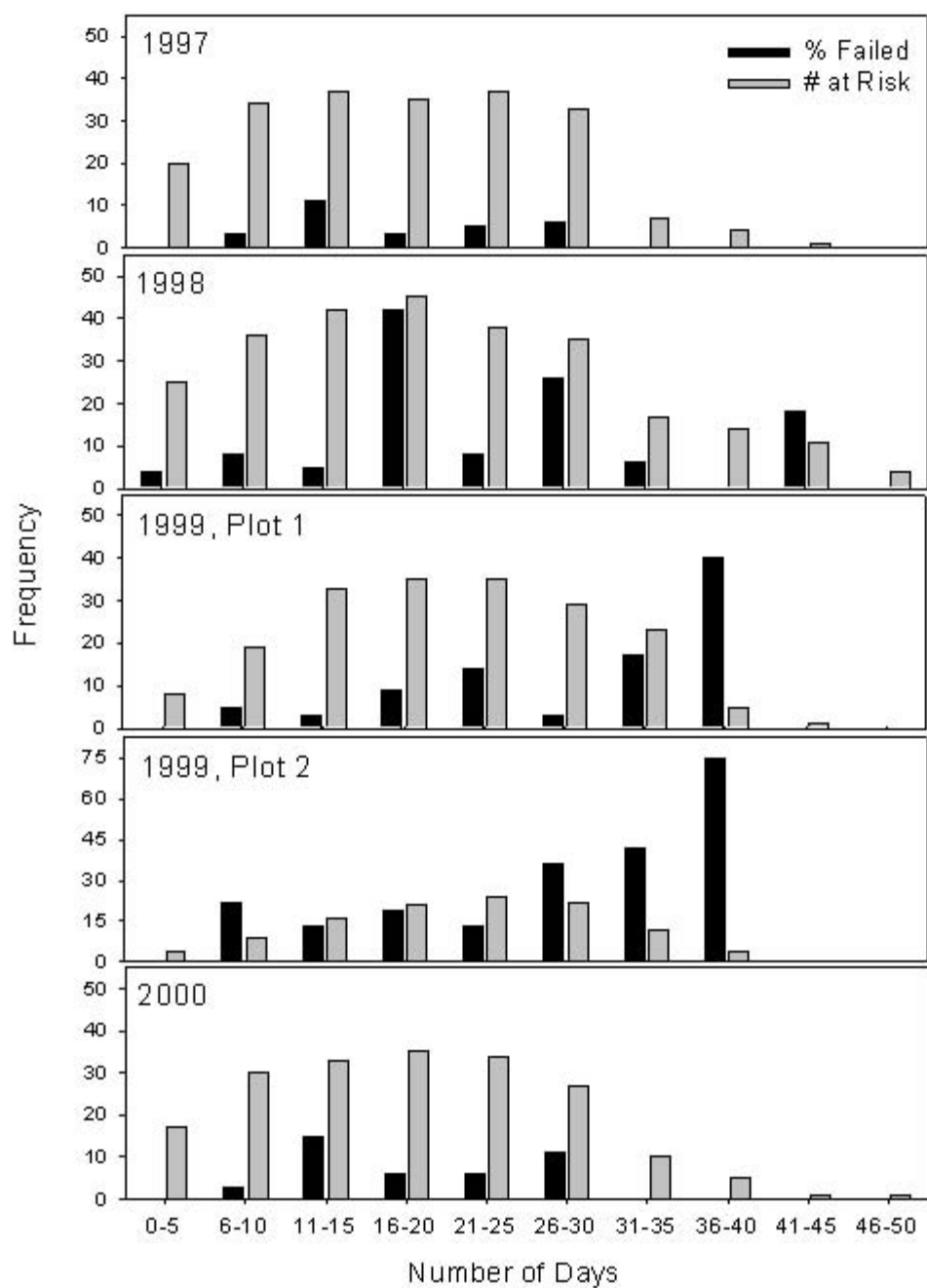
FIGURE 2.3. Percent of nest failures and number of nests at risk of failure in relation to number of days since the start of egg laying in each year for Yellow Warblers at Canvasback Lake, Alaska, 1997-2000.
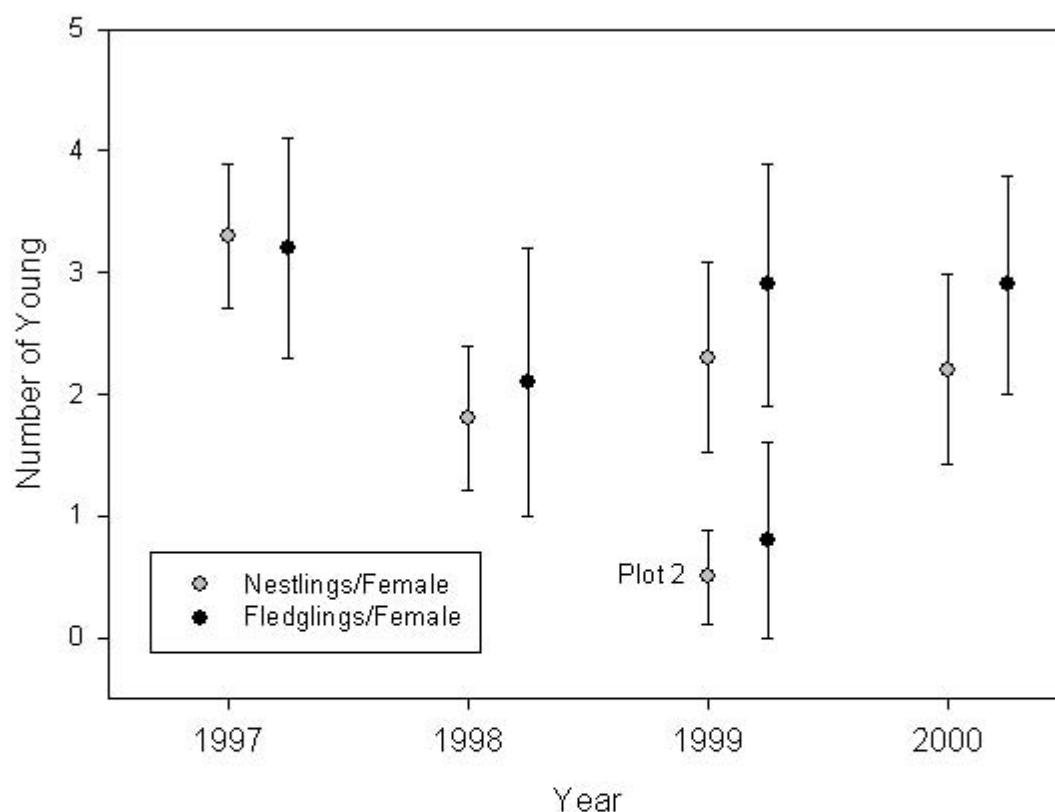
FIGURE 2.4. Comparison of two estimates of annual productivity for Yellow Warblers nesting at Canvasback Lake, Alaska, 1997-2000. Nestlings/female is mean number of nestlings observed during the final breeding attempt per female. Fledglings per female was the product of mean clutch size, percent egg viability, percent Mayfield nesting success, and number of breeding attempts per female. Estimates are shown with 95% confidence intervals.
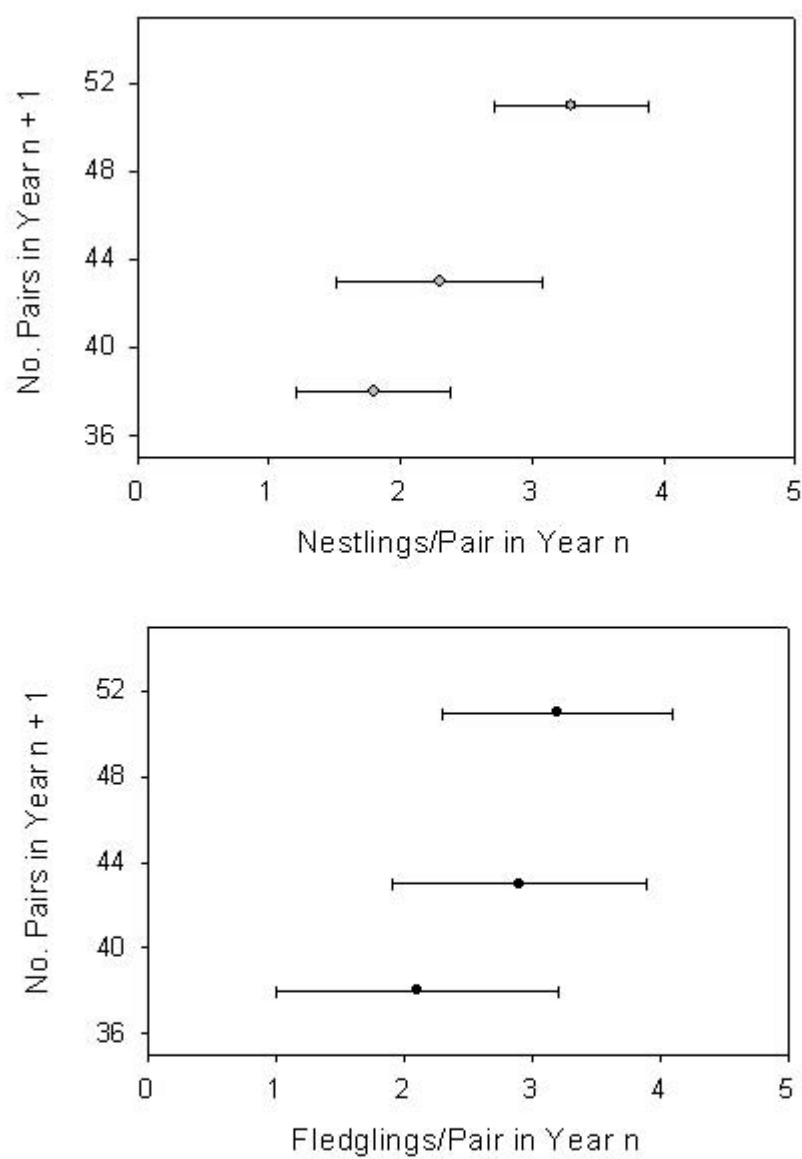
FIGURE 2.5. Relationship between annual productivity in one year and the number of breeding pairs in the following year for Yellow Warblers nesting at Canvasback Lake, Alaska, 1997-2000.
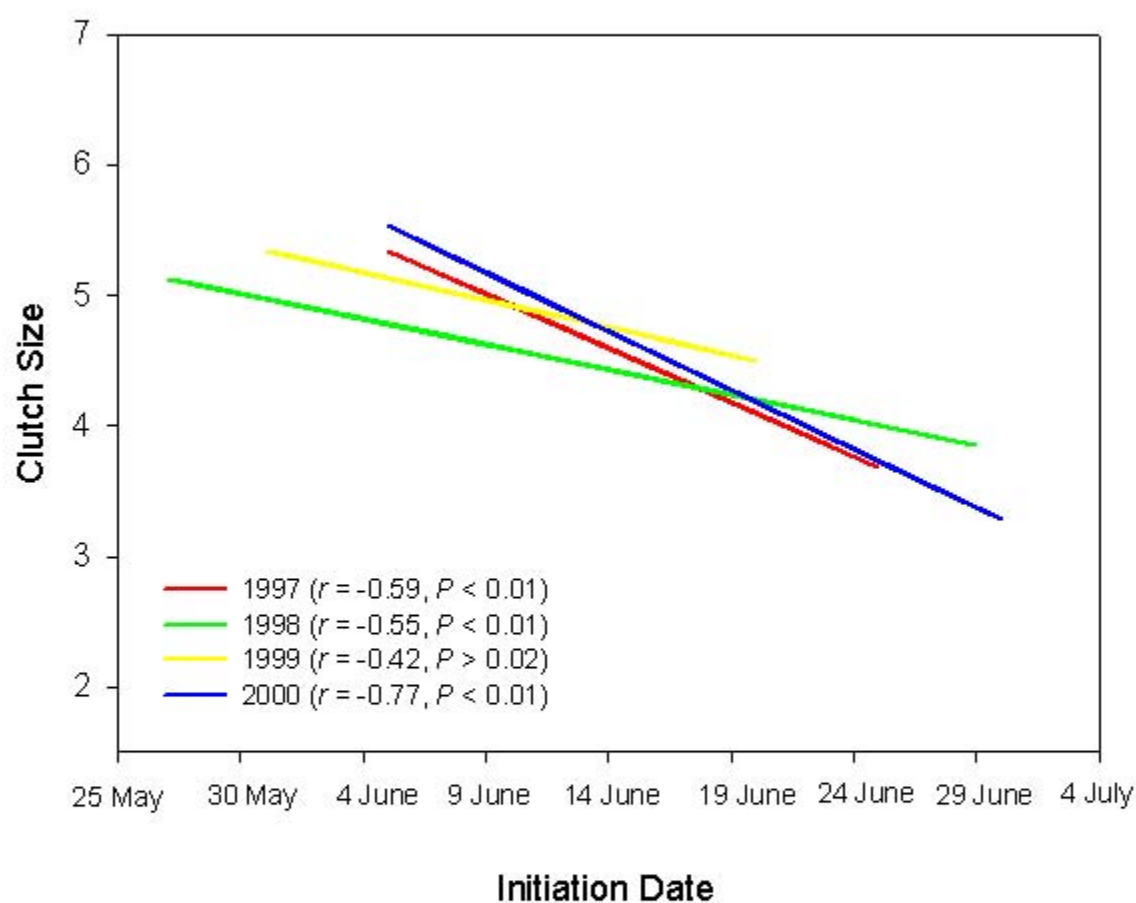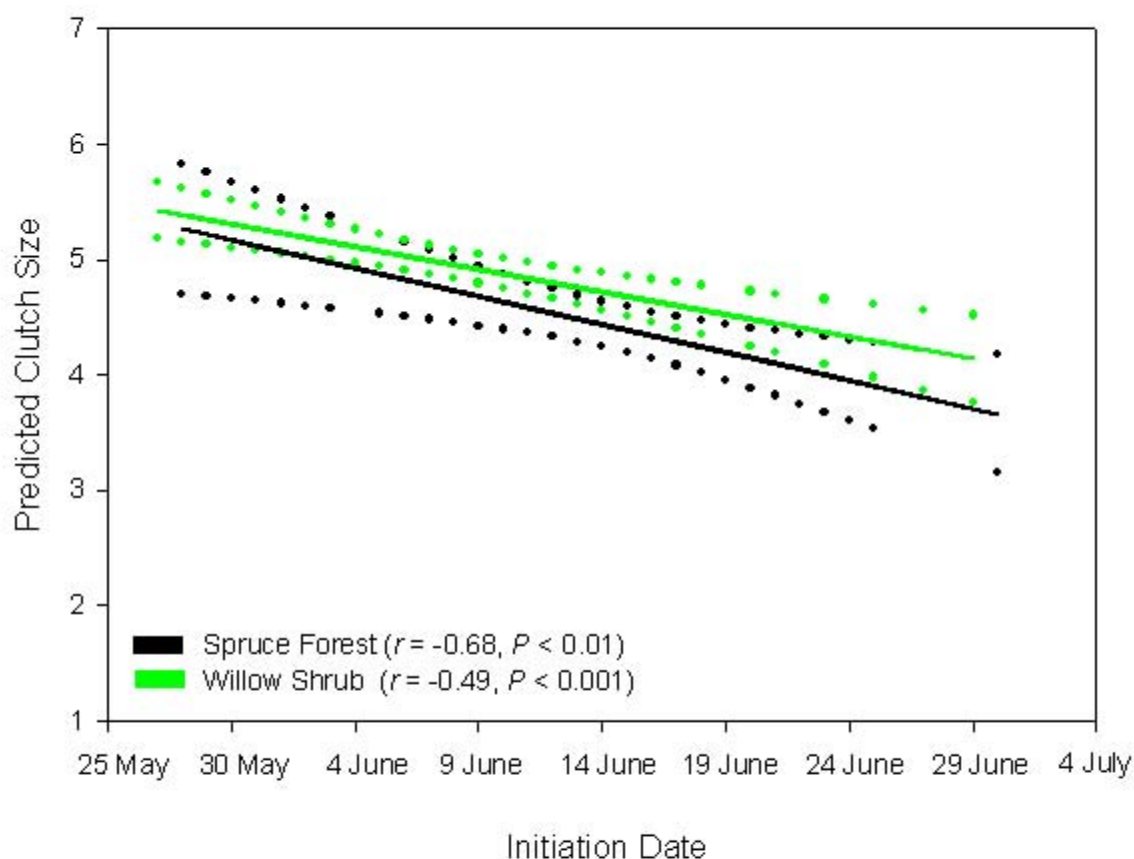
FIGURE 2.6. Relationship of clutch size to clutch initiation date and habitat for Yellow Warblers nesting on Plot 1 at Canvasback Lake, Alaska, 1997-2000. Results of linear regression analysis. Predicted clutch sizes are displayed as lines and their 95% confidence limits as dots.

TABLE 2.1. Reproductive success and annual productivity of Yellow Warblers by plot and year at Canvasback Lake, Alaska, 1997-2000. Means are shown with standard errors.

	Year	First Clutches[a]	Replace-ments (%)	n	Mean Clutch Size[b]	n	Mean Brood Size[c]	n	Nestlings/Nest[d]	n	Nestlings/Female[e]	Fledglings/Female[f]
Plot 1	1997	41	5 (11)	26	4.8 ±0.1	15	4.7 ±0.2	43	3.0 ±0.3	39	3.3 ±0.3	3.2 ±0.5
	1998	51	21 (29)	41	4.7 ±0.1	6	4.0 ±0.4	69	1.3 ±0.2	48	1.8 ±0.3	2.1 ±0.6
	1999	38	8 (17)	28	5.0 ±0.1	9	4.2 ±0.3	42	1.9 ±0.3	34	2.3 ±0.4	2.9 ±0.5
	2000	43	8 (16)	26	4.8 ±0.1	3	5.3 ±0.3	37	1.7 ±0.3	29	2.2 ±0.4	2.9 ±0.5
	All Yrs	173	42 (20)	121	4.8 ±0.1	33	4.5 ±0.1	191	1.9 ±0.2	150	2.4 ±0.2	2.6 ±0.5
Plot 2	1999	39	4 (9)	26	4.7 ±0.1	1	5.0	39	0.4 ±0.2	35	0.5 ±0.2	0.8 ±0.4

[a] Number of first breeding attempts. This number is considered equivalent to the number of breeding pairs.

[b] Known clutch size (observed after clutch completion and before hatching).

[c] Known brood size within two days of fledging.

[d] Mean number of nestlings/nest for all nesting attempts.

[e] Mean number of nestlings observed per final breeding attempt per female per year. Includes brood sizes where exact number of young uncertain (e.g., could be 4-6 young in nest but the smaller number was used for calculations).

[f] Product of number of clutches initiated per female (total number of clutches/total number of females), mean egg viability (93%), mean clutch size, and nest success. Standard error estimated by delta method (Oehlert 1992).

TABLE 2.2. Number and density of breeding pairs of Yellow Warblers at Canvasback Lake, Alaska. Densities are shown for each study plot, year, and habitat. Means are shown with standard errors[a].

Plot	Year	Spruce Forest[b]		Willow Shrub[c]		Willow-Spruce Edge[d]	
		# Pairs	Density (prs/ha)	# Pairs	Density (prs/ha)	# Pairs	Density (prs/ha)
1	1997	9	3.3 ± 0.04	20	7.1 ± 0.10	13	$3.8 \pm <0.01$
	1998	16	5.9 ± 0.07	22	7.9 ± 0.11	13	$3.8 \pm <0.01$
	1999	8	3.0 ± 0.03	20	7.1 ± 0.10	10	$2.9 \pm <0.01$
	2000	10	3.7 ± 0.04	21	7.5 ± 0.11	12	$3.5 \pm <0.01$
	Mean		4.0 ± 0.04		7.4 ± 0.11		$3.5 \pm <0.01$
2	1999	9	$1.3 \pm <0.01$	15	$6.3 \pm <0.01$	15	$4.3 \pm <0.01$

[a] Standard errors are underestimated because of unmeasured error in the area measurements.

[b] Forest habitats included white spruce forest or mixed white spruce and quaking aspen forest and comprised 2.7 ± 0.03 ha on Plot 1 and 7.1 ± 0.02 ha on Plot 2.

[c] Shrub habitats included tall or medium willow shrub thickets and comprised 2.8 ± 0.04 ha on Plot 1 and 2.4 ± 0.02 ha on Plot 2.

[d] Willow-spruce edge habitats comprised $3.4 \pm <0.01$ ha on Plot 1 and 3.5 ± 0.01 ha on Plot 2.

TABLE 2.3. Results of ANCOVA relating clutch size to year and habitat. Clutch initiation date was the covariate. Data were analyzed for clutches on Plot 1 at Canvasback Lake, Alaska, 1997-2000.

Variable	Full Model (n = 120)			Reduced Model		
	df	*F*	*P*	df	*F*	*P*
Model	71	2.78	< 0.001	60	2.85	< 0.001
Year	3	0.34	0.79	3	1.23	0.31
Habitat	1	1.50	0.23			
Initiation Date	29	2.43	< 0.01	29	3.47	<0.001
Initiation Date x Year	26	2.34	< 0.01	28	2.13	<0.01
Initiation Date x Habitat	10	1.32	0.25			

TABLE 2.4. Evidence of failure for Yellow Warbler nests at Canvasback Lake, Alaska, 1997-2000.

Probable Cause	Evidence of Failure	No. of Nests
Weather	Under construction; observed damaged after strong winds	1
Adult Mortality	Female disappeared during hatching, male still present	1
Disturbance	Abandoned by female during construction	4
Predation	Depredated by red squirrel (observed)	1
	Clutch reduction, later nest empty	3
	Egg shell pieces present; nest damaged or lining disturbed	12
	Egg shell pieces present; nest undamaged	23
	Nest empty prematurely; nest damaged or lining disturbed	30
	Nest empty prematurely; nest undamaged	41
Unknown	Nest empty and undamaged; unclear if any eggs were laid	3
	Brood reduction; later nest empty	2
	Female dismantling nest to build another nest	3
	Nest removed from tree or shrub	11
	No activity observed during several visits to nest	6
Total		141

TABLE 2.5. Maximum likelihood estimates of coefficients and associated statistics from proportional hazards regression of Yellow Warbler nest success. A stepwise model selection procedure was used to select best variables at a significance of $P < 0.10$.

Model	Sample	Selected Variables	Coefficient	SE	Chi-Square	P	Hazard Ratio
Spatial and Temporal[a]	All Nests[b]	Plot	1.28	0.27	21.96	< 0.001	3.61
		Year 1998	0.77	0.25	9.78	< 0.01	2.17
Temporal[c]	Plot 1	Year 1998	0.76	0.25	9.40	< 0.01	2.14
Habitat[d]	Plot 1	Year 1998	0.83	0.24	12.08	< 0.001	2.30
		W-S Edge	0.74	0.24	9.20	< 0.01	2.10
		Habitat	-0.41	0.24	2.76	>0.09	0.67

[a] Variables tested included plot, a dummy variable for each year (1997-2000), and clutch initiation date.

[b] Includes nests from Plot 1, 1997-2000 and Plot 2, 1999.

[c] Variables tested included a dummy variable for each year (1997-2000) and clutch initiation date.

[d] Variables tested included a dummy variable for each year (1997-2000), habitat (spruce forest or willow shrub), and edge (yes or no). Two types edge variables were tested, one for willow-spruce edge and one for the edge of a lake or meadow.

TABLE 2.6. Nest success of Yellow Warblers by plot, habitat, and year at Canvasback Lake, Alaska, 1997-2000.

	Year	n[a]	Losses	Exposure[b]	DSR[c]	SE[d]	Mayfield[e]	95% CI
Plot 1	1997	43	10	609.5	0.984	0.005	70%	(55,87)
	1998	68	41	941.5	0.957	0.007	38%	(27,51)
	1999	40	16	662.5	0.976	0.006	58%	(44,76)
	2000	43	13	627.5	0.979	0.006	63%	(49,81)
	1997-2000[f]	194	80	2841.0	0.972	0.003	53%	(46,61)
Plot 2	1999	35	28	403.0	0.931	0.013	21%	(11,37)
Shrub	1997	26	4	364.5	0.989	0.006	78%	(62,99)
	1998	42	25	607.0	0.959	0.008	40%	(27,57)
	1999	29	10	489.0	0.980	0.006	64%	(48,84)
	2000	27	5	422.0	0.988	0.005	77%	(61,97)
	1997-2000[f]	124	44	1882.5	0.976	0.004	59%	(51,69)
	1999, Plot 2	26	22	286.5	0.923	0.016	17%	(8,35)
Forest	1997	17	6	245.0	0.976	0.010	58%	(37,89)
	1998	26	16	334.5	0.952	0.012	34%	(20,57)
	1999	12	7	175.0	0.960	0.015	41%	(21,78)
	2000	17	9	207.0	0.957	0.014	38%	(20,71)
	1997-2000[f]	72	38	961.5	0.960	0.006	41%	(31,54)
	1999, Plot 2	9	6	116.5	0.949	0.021	31%	(12,78)

[a] Number of nests under observation and included in Mayfield calculations.

[b] Number of days nests were under observation.

[c] Mean daily nest survival rate calculated by Mayfield method (Mayfield 1961, 1975).

[d] Standard errors of DSRs calculated according to methods of Johnson (1979).

[e] Mayfield nest survival rate for entire nesting period (22 days) with 95% confidence intervals.

[f] Mean DSR weighted by days of exposure.

TABLE 2.7. Reproductive success and annual productivity of Yellow Warblers by year and habitat on Plot 1 at Canvasback Lake, Alaska, 1997-2000. Means are shown with standard errors.

Year	Habitat	First Clutches[a]	Replacements (%)	n	Mean Clutch Size[b]	n	Mean Brood Size[c]	n	Nestlings per Nest[d]	n	Nestlings per Female[d]	Fledglings per Female[e]
1997	Willow	25	2 (7)	16	5.0 ±0.2	12	4.8 ±0.2	27	3.5 ±0.4	26	3.5 ±0.4	3.8 ±1.0
	Spruce	16	3 (16)	10	4.5 ±0.2	3	4.7 ±0.3	16	2.1 ±0.6	15	2.8 ±0.6	2.4 ±0.8
1998	Willow	31	13 (30)	33	4.8 ±0.1	5	4.0 ±0.4	42	1.4 ±0.3	32	1.9 ±0.4	2.4 ±0.6
	Spruce	20	8 (29)	8	4.3 ±0.2	1	4.0	27	1.0 ±0.3	21	1.7 ±0.4	1.6 ±0.9
1999	Willow	27	5 (16)	22	5.1 ±0.1	8	4.4 ±0.3	29	2.3 ±0.4	26	2.6 ±0.4	3.2 ±0.5
	Spruce	11	3 (21)	6	4.5 ±0.2	1	3.0	13	0.8 ±0.4	10	1.4 ±0.6	1.9 ±0.9
2000	Willow	28	1 (3)	19	5.0 ±0.2	2	5.5 ±0.5	20	2.4 ±0.5	17	2.6 ±0.5	3.7 ±1.0
	Spruce	15	7 (32)	7	4.4 ±0.3	1	5.0	17	0.9 ±0.4	12	1.6 ±0.6	1.5 ±1.2
All Yrs	Willow	111	21 (16)	90	4.9 ±0.1	27	4.6 ±0.2	118	2.3 ±0.2	101	2.6 ±0.2	3.1 ±0.5
	Spruce	62	21 (25)	31	4.4 ±0.1	6	4.3 ±0.3	73	1.2 ±0.2	58	1.9 ±0.3	1.8 ±0.4

[a] Number of first breeding attempts. This number is considered equivalent to the number of breeding pairs.

[b] Known clutch size (observed after clutch completion and before hatching).

[c] Known brood size within two days of fledging.

[d] Mean number of nestlings/nest for all nesting attempts.

[e] Mean number of nestlings observed per final breeding attempt per female per year. Includes brood sizes where exact number of young uncertain (e.g., could be 4-6 young in nest but the smaller number was used for calculations).

[f] Product of number of clutches initiated per female (total number of clutches/total number of females), mean egg viability (93%), mean clutch size, and nest success. Standard error estimated by delta method (Oehlert 1992).

TABLE 2.8. Densities of Yellow Warblers breeding at various locations in North America.

Location	Pairs/ha	Habitat	Study
Delta Marsh, Manitoba	14.4	Wetland-deciduous forest-willow shrub	Goossen and Sealy (1982)
Northwest Iowa	6.2	Lake margin with mixed shrub	Kendeigh (1941)
Rhode Island	5.0	Moist shrub	Mitra (1999)
Southeast Ontario	3.9	Mixed riparian shrub	Yezerinac et al. (1999)
Plot 1, Canvasback Lake	**3.6**	Lakeshore spruce forest and willow shrub	This study
Southern Wisconsin	3.5	Park with mixed shrubs	Young (1949)
Plot 2, Canvasback Lake	**2.7**	Lakeshore spruce forest and willow shrub	This study
James Bay, Ontario	2.2	Coastal wetland willow and alder shrub	Rimmer (1988)
Southeast Michigan	2.2	Wet shrub thicket and old pasture	McGeen (1972)
Southeast Ontario	1.8	Mixed riparian shrub	Clark and Robertson (1979)
Southeast Michigan	1.7	Mixed deciduous tree and shrub	DellaSala (1985)
Churchill, Manitoba	0.7	Riparian willow scrub and lake margins	Briskie (1995)
Southern Michigan	0.2	Wetland shrub and field edge	Batts (1961)
Mean ± SE[a]	3.8 ± 1.2		

[a] Mean and standard error, excluding the nests from Canvasback Lake.

TABLE 2.9. Nest success of Yellow Warblers at various locations in North America. The shaded area includes estimates that are within the 95% confidence interval for nest success on Plot 1 at Canvasback Lake, Alaska in 1997-2000.

Location	Type[a]	# nests	# years[b]	Nest Success	Study
Southeast Alaska	Mayfield	68	3	0.65	Willson & Gende (2000)
Southern Manitoba	Apparent	118	2	0.58	Weatherhead (1989)
Canvasback Lake, Plot 1	Mayfield	194	4	0.53	This study
Southern Manitoba (unparasitized)	Apparent	169	3	0.53	Goossen & Sealy (1982)
Rhode Island	Mayfield	[c]	4	0.51	Mitra (1999)
Sierra Nevada, California	Mayfield	78	2	0.52	Cain et al. (2003)
Northern Manitoba	Mayfield	61	6	0.49	Briskie (1995)
Southeast Ontario	Apparent	109	3	0.38	Clark & Robertson (1979)
West Montana - agricultural	Mayfield	266	2	0.36	Tewksbury et al. (1998)
West Montana - forested	Mayfield	24	2	0.29	Tewksbury et al. (1998)
Southern Manitoba (parasitized)	Apparent	58	3	0.24	Goossen & Sealy (1982)
Canvasback Lake, Plot 2	Mayfield	35	1	0.21	This study
Mean ± SE[d]				0.45 ± 0.04	

[a] Type of estimate: Mayfield (nest survival rate calculated by Mayfield method) or
  Apparent (percentage of nests found that successfully fledged at least one young).

[b] Number of years data was collected.

[c] Exact sample size used for Mayfield calculations unknown but between 40 and 94.

[d] Overall mean and standard error, excluding the nests from Canvasback Lake.

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APPENDIX 2.1. Aerial photos of Plot 1 (top) and Plot 2 (bottom) at Canvasback Lake, Alaska.

CONCLUSION

The reproductive ecology of Yellow Warblers breeding at Canvasback Lake was similar in many respects to that of other populations of Yellow Warblers that have been studied, but the location of the study site at a relatively high latitude and some unconventional habitat use resulted in several distinct differences. The breeding season at Canvasback Lake was restricted, but a continental climate ensured that it was not as limited as other locations of similar latitude. Overlap of the onset of pre-basic molt and fledgling care also effectively extended the breeding period. In common with all other populations of Yellow Warblers, females attempted to raise only a single brood in a season, polygynous pairings occurred at low frequency, and clutch size declined as the season progressed. Some females attempted to replace lost clutches or broods, but the frequency of clutch replacement was constrained by the brevity of the breeding season in east central Alaska. More clutches were replaced during a season with an early onset of breeding. Following a common trend in many avian species, clutch size tended to be higher than in lower latitude populations of Yellow Warblers. Hatching success of eggs that survived the incubation period was similar to that of other populations of passerines. Breeding density and nest success rates were in the middle of the range of values observed for other Yellow Warbler populations. As for many populations of passerines, nest predation was likely the principle cause of nest failures. Although cowbird parasitism has a major impact on the productivity of many populations of Yellow Warblers, Canvasback Lake was beyond the breeding range of this species and

brood parasitism did not occur at the study site. Too little information is known about mean annual productivity per female to make comparisons among populations, but fledgling production at the study site did not appear to be unusually high or low. Hatching success of eggs that survived the incubation period was similar to that of other populations of passerines. Many of the pairs at Canvasback Lake nested in willow shrub and forest edge habitats, typical breeding habitats for Yellow Warblers in North America, but a considerable portion of the study population also nested in spruce forest. Additional detailed information is needed about the reproductive ecology of Yellow Warblers at a variety of locations to enable more meaningful comparisons among populations.